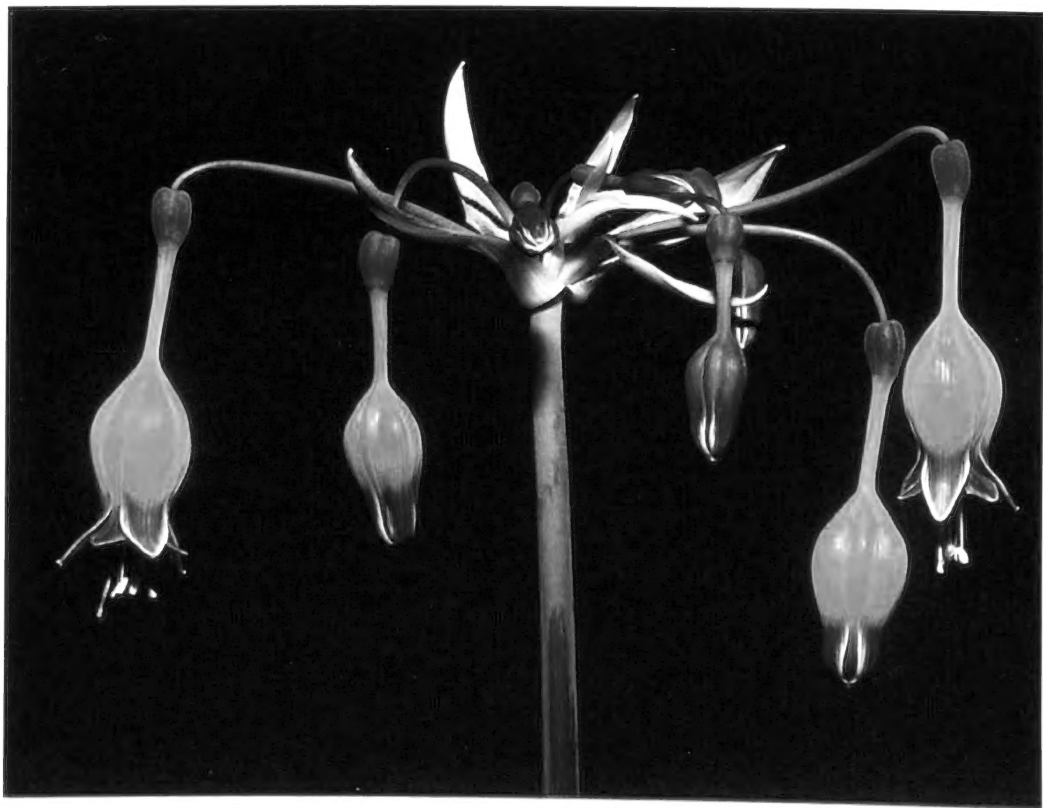

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Alan W. Meerow • Editor

Susannah Levy • Layout and Design

Arnold Trachtenberg • Managing Editor

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EDITOR'S NOTES

The World Conservation Union (IUCN) Red List of Threatened Plants reports that nearly 34,000 species, 12 percent of the world's vascular plants, are threatened with extinction. More than 7,000 volunteers of the IUCN Species Survival Commission's (SSC) various taxonomic specialist groups contributed to the creation of this list (and a similar one for animals), probably the most recognized publications relating to conservation. The Bulb Specialists Group of the SSC was formed in 1998. The committee currently includes representatives from the United States, Brazil, South Africa, and the United Kingdom, and encompasses scientists, botanical garden staff members, commercial horticulturists, and knowledgeable hobbyists. The mission of the Bulb Specialists Group include: 1) the review and revision of the Red List of Threatened Plants as it relates to geophytic plant groups; 2) determination of the critical areas where geophytes are being marketed directly from the wild, both the source and destination; 3) the review of current ex situ propagation and production programs for valued bulbs, such as the those ongoing in Turkey. Are they working? Have they made a dent in traffic of wild-collected material? Can they be expanded? Can they serve as a model for export to other geophyte rich areas of the world? And 4) determining if centralized germplasm repositories represent a feasible endeavor for bulbous plants, particularly those rescued from development. In concert with ex situ propagation and production efforts, can they even be sources of revenue for further conservation efforts? Ultimately, the group will produce an Action Plan that will detail our recommendations for the conservation and preservation of global geophytic diversity.

As I write this, "The Magic of Bulbs" looms near on the horizon, the 2002 symposium of the International Bulb Society. We will be meeting at the illustrious Huntington Botanical Garden this year, and, in addition to a wealth of presentations by geophyte aficionados, we can look forward to one of California's most inspirational botanical landscapes.

Volume 56 (2001) of HERBERTIA arrives a bit later into 2002 than I would have preferred, but an unexpected detour into the editorship of BULBS, our twice annual magazine, delayed completion of the Journal. Henceforth, HERBERTIA will be scheduled to appear within the first quarter of the year following the volume date. The reason for this is to allow me to complete a full year's bibliography of geophyte-relayed scientific literature.

This issue of HERBERTIA brings together articles on bulbs from both the temperate and tropical zones by an international array of scientists. I am always gladdened by the response that I receive from colleagues when I rather unabashedly beg for a contribution from them for this journal. I also thank Amna Ahmad, Sean Graham, Spencer Barrett, Julie Dutilh and Reinhard Fritsch for each reviewing manuscripts that were submitted.

Congratulations to our Herbert Medalist for 2001, Graham Duncan. Graham is well known around the world for his many writings on South African geophytes, and his skill as a grower of same.

Please note that the final deadline for submissions for volume 57 (2002) of HERBERTIA is November 1, 2002.

—Alan W. Meerow, Editor

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THE HERBERT MEDAL



The Herbert Medal is the highest honor that the International Bulb Society can bestow upon a person for meritorious achievement in advancing the knowledge of bulbous plants. The medal is named for William Herbert (1778-1847), son of Henry Herbert, Earl of Carnarvon. William Herbert had a predilection for amaryllids and achieved success in their hybridization. He published his research findings in several monumental works. His contributions as a pioneer geneticist and plant breeder, and his arrangement of the Amaryllidaceae, helped set the stage upon which other workers, both amateur and professional, have been able to advance.

The award includes honorary life membership in the Society.

The Herbert Medal may be awarded annually or on special occasions by the Board of Directors of the Society. Medalists need not be members of the Society to be considered for the Herbert Medal.

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2001 HERBERT MEDALIST GRAHAM DUGALD DUNCAN



I was born in November 1959 and raised on the Cape West Coast in the small fishing village of Saldanha, where my interest in wild-flowers in general, and bulbous plants in particular, began. From a very young age I was consumed by the astonishing diversity of wild flowers that surrounded me everywhere, as well as by the will to cultivate plants. In those early days, Saldanha was an unspoiled, little-known floral paradise, where my interest in my natural surroundings was shared and enthusiastically encouraged by my mother. The surrounding granite outcrops and sandy flats, with their wealth of annuals and bulbous species became my stamping ground, and at no stage was there any doubt as to which direction my future career would turn. From the age of 11, I attended boarding school at the South African College School in Cape Town, from which I matriculated.

After my parents relocated to Cape Town, I grew bulbs cultivated in a tiny collapsible wooden greenhouse (incidentally, currently still in use after several moves) in Newlands, close to Kirstenbosch Botanical Gardens. I exhibited my plants at the local wildflower shows held at Kirstenbosch, and decided that Kirstenbosch was the place where I wanted to be. In 1979 I enrolled at the Cape Technikon for the National Diploma in Horticulture, which I attended on a part-time basis, and at the same time joined the horticultural staff at Kirstenbosch Botanical Gardens. At first I worked there as an unpaid student-horticulturist, then as a paid student employee, and later took charge of the bulbous plants collection as a qualified horticulturist, where I have remained ever since! It was indeed fortunate that from my very first day of employment at Kirstenbosch, I was allowed to work almost exclusively on my chosen group, namely bulbous plants.

I attribute my special interest in the genus *Lachenalia* to my early days at Saldanha, where *Lachenalia rubida* once grew by the thousands on the sand dunes just above the high water mark, literally on the doorstep of our family home on Beach Road. I benefited greatly from the vast wealth of knowledge acquired by Miss W.F. Barker, first Curator of the Compton Herbarium at

Kirstenbosch, over several decades of research on the genus *Lachenalia*. By the mid 1980's I felt confident enough to begin work on a popular guide to the genus, published in 1988 as **The Lachenalia Handbook**, illustrated almost entirely with my own photographs, and which is volume 17 of the Annals of Kirstenbosch Botanic Gardens series.

It has been a wonderful, and intensely satisfying privilege to spend the past 21 years working below majestic Castle Rock at Kirstenbosch Gardens, surely the most beautiful setting for a botanic garden in the whole wide world. My work at Kirstenbosch entails curating the very large living collection of indigenous South African bulbous plants. These are mainly housed under cover in the nursery for protection from the excessive winter rainfall. The generally poorly-drained soil in the garden itself, as well as the depredations of those stealthy night-creatures the porcupines, and of course the mole rats, are further reasons for the bulk of the bulb collection being housed in the nursery. The bulbs are grown in sturdy raised beds or in pots. Due to the rapid urbanization of the Cape Flats around Cape Town, as well as to agricultural expansion in the Western and southwestern Cape, countless indigenous bulbous species are now either in perilous threat of extinction in the wild, or have had their numbers reduced to such an extent that their future in the wild state is anything but secure. A large number of these endangered species, almost all endemic to this region, form part of the living collection in the bulb nursery, where they are carefully propagated, seed distributed worldwide, and where feasible, re-introduced into the wild. The recent construction of the Botanical Society Conservatory at Kirstenbosch has made it possible to exhibit representatives of the wealth of arid succulent southern African flora to the public. The structure comprises four specialist display units, one of which is the Kay Bergh Bulb House, where a permanent planting of evergreen South African bulbs, as well as a changing display of container-grown bulbs from the nursery just up the hill, provides interest throughout the year. Indeed, at least one bulbous species is to be seen in flower in the Bulb House every single day of the year, with the peak display season extending from the end of July until the end of October.

My work at Kirstenbosch also center around introducing bulbous species with horticultural potential to the public, and in this regard, I refer particularly to my work with the genera *Lachenalia*, *Moraea*, *Clivia*, *Veltheimia* and the deciduous *Agapanthus* species.

Although I have never found writing easy, and to be quite frank would much rather have soil in my hands rather than a pen or computer keyboard, I do feel compelled to share knowledge when it may be of use to others. In the course of my writings, I have been able to illustrate some of my published work with my own photographs, and in 1991 I received the Botanical Society of South Africa's Schelpe Award for a series of articles dealing with the cultivation of the genus *Cyrtanthus*. I have also had the privilege of working with some of this country's most talented contemporary botanical artists. The artist Elise Bodley, who illustrated *Bulbous Plants of Southern Africa*, co-authored by Prof. Niel Du Plessis and myself, was honored in having all her plates from this book exhibited in the United States at the Smithsonian Institution's National Museum of Natural History. Her work was also accepted at the Hunt Institute of Botanical Documentation in Pittsburgh, and at the Audubon Naturalist Society. The text and illustrations of *Bulbous Plants of Southern Africa* received Nasionale Pers's Recht Malan Prize for non-fiction in 1990.

I have been fortunate in travelling fairly widely due to my interest in bulbous plants. I spent a three-month period working with the bulb collection at the University of California, Irvine's Arboretum, and have attended and presented papers at the three most recent International Society for Horticultural Science's Symposia on Flowerbulbs, held in Poland, Israel, and South Africa, respectively. I greatly enjoyed serving on the Organizing Committee of the 2000 Symposium in Cape Town. I have represented Kirstenbosch at the Chelsea and Hampton Court Flower Shows in England, and recently had the very good fortune to travel to South America (Peru, Bolivia, and Chile) with bulb expert Dennis Tsang, where bulbous species from that continent were studied and enjoyed in the wild. A very recent trip to Japan, in which I took part in seminars dealing with the cultivation and propagation of South African bulbous plants, really brought home to me the truly international appeal of South Africa's geophytes.

I am currently working on a cultivation guide to the genus *Nerine*, which will form part of the Kirstenbosch Gardening Series, as well as an M.Sc. degree dealing with the taxonomy of the genus *Lachenalia*.

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THE HAMILTON P. TRAUB AWARD FOR DISTINGUISHED SERVICE

This award was established in 2000 by the IBS Board of Directors to recognize meritorious service to the Society. It is named after Dr. Hamilton P. Traub, founder of the American Plant Life Society, antecedent of IBS, and editor of its journal for a half century.

2001 TRAUB AWARD MARVIN ELLENBECKER



Marvin Ellenbecker was born on November 9, 1942, in Appleton, Wisconsin. He has been collecting bulbs since his early years, and joined the American Plant Life Society in 1957. After working as an accountant, he earned a degree in ornamental horticulture at the University of Wisconsin-Madison, followed. In 1972, he was selected as a summer student at Longwood Gardens in Kennett Square, Pennsylvania, and wrote a paper for the Longwood Summer

Program on *Paramongaia weberbaurei* (later published in the 1973 issue of *Plant Life*). He completed a Masters Degree at Michigan State University in park administration. He worked after graduation for the Virginia Extension Service as Extension Agent for Alleghany County, Virginia, followed by the position of horticulturist with the Dallas Park and Recreation Department. He later became Park Supervisor in charge of the State Fair Park District in Dallas. Eight years later, he became the Urban Forester (Landscape Development Associate) for the City of Santa Ana, California Planning and Building Agency. Marvin has served in the past as both IBS Seed List Coordinator and Curator of Living Collections.

TAXONOMY OF THE GENUS *ALLIUM* L.: CONTRIBUTIONS FROM IPK GATERSLEBEN

Reinhard M. Fritsch

Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK)
Gatersleben, Land Sachsen-Anhalt, Germany

INTRODUCTION

From its founding as “Kaiser Wilhelm Institut für Kulturpflanzenforschung” in 1943, a Taxonomic Department has always been an integral part of the institution which is now called Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK, Institute of Plant Genetics and Crop Plant Research, a non-profit governmental research institute) located at Gatersleben, Land Sachsen-Anhalt, in Germany. Initially the main activities were devoted to creating formal infraspecific morphological classifications of important crop species of temperate regions in order to classify the (at that time still) huge diversity of land races and primitive cultivars. Later, the research activities centered on the more complex relations between morphology, evolution, classification and nomenclature of cultivated plants and their close relatives. Both taxonomic research on important crop species (Fritsch et al., 1977; Meyer, 1980; Schultze-Motel and Meyer, 1981) as well as compilation of world manuals of cultivated species (Hanelt, 2001; Mansfeld, 1959; Schultze-Motel, 1966, 1986) are part of the research profile of the IPK Taxonomic Department.

In the early 1980's a research program was set up to deal with the taxonomically difficult genus *Allium*. Beside common onion and garlic, plants of world-wide economic importance, about two dozen species are reported to be under cultivation as spice, medicinal, or vegetable plants (Fritsch and Friesen, 2002; Hanelt, 2001). However, different scientific names and several more or less contradictory classifications were applied to them in the literature, and different views on their relationships, wild precursors and closely related wild species were presented in different handbooks and scientific papers. Therefore, research was started to investigate the morphological, anatomical, developmental, karyological, and phytochemical characters of a broad array of *Allium* taxa.

Several research groups worldwide concentrate on *Allium* species. A substantial part of their results has been summarized in the Proceedings of an *Allium* Symposium held at Gatersleben in 1991 (Hanelt et al., 1992), which

was partly updated in 1996 (Fritsch, 1996a). More recently, the current state of a few general and special aspects were presented during an *Allium* symposium organized by the Munich Botanic Garden in 2000 (Kretschmer, 2001). A recent onion handbook (Rabinowitch and Currah, 2002) presents the main principles of modern *Allium* science in general, as well as a wide spectrum of information about agricultural traits etc. of the economically most important species and groups.

THE LIVING ALLIUM COLLECTION

Allium is an extremely diverse genus comprising more than 700 species almost exclusively distributed in the northern hemisphere. This number is based on our experience in recognizing *Allium* species as living plants in the wild and under cultivation, as well as from dried herbarium specimens, in addition to independent estimates given in the literature. About 700 additional species names should be regarded as synonyms (Gregory et al., 1998).

Traditional studies in plant taxonomy are mainly based on dry specimens housed in herbaria. In the genus *Allium*, herbarium specimens of most taxa do not show all characters necessary for an exact determination. Apart from a few groups, most species are adapted to arid climates. Because of their overall ephemeral life form, these plants show an extremely accelerated annual life cycle, producing well-developed leaves only prior to anthesis. The leaves are usually dry or withered when the plants are in full flower. Moreover, floral parts are strongly withered when the capsules develop. Well-functioning protection against water loss is effective even in the herbarium press, and plants may continue development as long as they are not fully dry. As a result, herbarium specimens may present flowers of malformed shape and color, or atypical capsule morphology, and may therefore simulate a species with a long flowering period.

A living collection of many different taxa is therefore an absolutely essential basis for comprehensive taxonomic investigations. As initial stock, a selection of wild and cultivated *Allium* accessions from the Genebank collection of IPK was planted in a separate area. During the early and mid-1980's, many species were ordered by international seed exchange from botanical gardens and were added after their identification was confirmed.

However, the most important accessions have been collected during research missions conducted jointly with foreign partner institutions. Nearly all coworkers of the IPK Taxonomy and Genebank Departments took part in these missions, and several colleagues from other institutions sent us

materials of wild offspring. Details of our collecting activities (Hammer et al., 1995) and the state of the collections (Hanelt, 1996a) have been reported a few years ago. More detailed statistical data about the development of our living collection are presented in a recent paper (Fritsch, 2002).

Over a period of about 15 years the working collection of the Taxonomy Department has expanded into the world's most comprehensive taxonomic *Allium* collection. Since the mid-1990's, about 340-360 *Allium* species and subspecies have been permanently present, with a total of about 2000 determined accessions (Fig. 1). In the last few years, the number of accessions was reduced to about 1750 without reducing the number of species. Because most *Allium* species occur naturally in warm-temperate to dry-subtropical regions (main center of diversity in Southwest and Middle Asia), this seems approximately the maximal number of species which can successfully be grown under the rather humid conditions of Central Europe. Members of all subgenera are present although not proportionally represented.

In the taxonomic collection, exclusively vegetatively maintained alliums like garlic often suffer from virus diseases (Graichen et al., 1992). Appropriate methods to establish *in vitro* collections of these accessions (Keller et al., 1995, 1997; Keller and Senula, 2001; Keller, 1991, 1992a, b; Senula and Keller, 2000) and to eliminate viruses through meristem culture and thermotherapy were developed (Keller et al., 1999; Senula et al., 2000).

MORPHOLOGY, DEVELOPMENT, AND PHENOLOGY

In the early 1980's, traditional morphological characters at the species level were used for numerical taxonomic analyses that resulted in heterogeneous clusters without taxonomic relevance. Only the addition of anatomical, chemical, karyological, and specific morphological data (like growth form etc.) as well as a higher number of OTU's (operational taxonomic units, in the given case species) resulted in moderately acceptable dendrograms. Both agglomerative and divisive methods gave similar results all with a few wrongly assigned species (Schultze-Motel, 1994). One of these dendrograms is presented in the proceedings of the 1991 *Allium* Symposium (Hanelt et al., 1992).

Branching system, leaf types, and their position in the leaf sequence were studied in the genus (Kruse, 1992a), which generally exhibits a sympodial, acrotonous ramification. The inflorescence terminates the shoot, which continues growth from the lateral bud in the axil of the uppermost leaf. Rhizomatous species develop few to several shoot generations of different

order and only rarely special storage leaves. Specialized leaf types and growth types were found in the subgenera *Amerallium* Traub, *Allium*, and *Melanocrommyum* (Webb et Berth.) Rouy. These possess only one or two extremely thickened storage leaves, thin cataphylls, and often a reduced number of foliage leaves.

In the genus *Allium*, more-or-less ovate to drop-shaped seeds are usual. They can be flattened and are often irregularly angled. However, seed shape is strongly influenced by seed (ovule) number and several morphological characters of the capsules and thus show wide variation. Additionally, my own observations (unpubl.) showed also that seed shape is influenced by the conditions during seed development. There are often clearly visible differences between seeds harvested in different years. This may be the reason that seed shape is only rarely presented in taxonomic treatments, although it is often a species-specific character (e.g. Wilde-Duyfjes, 1976). In subg. *Melanocrommyum*, section-specific differences in seed shape exist (Fritsch, 1992a).

More data are available to characterize seed size as expressed by seed weight. Examination of more than 100 species showed considerable variation within the genus *Allium*, but a rather good correlation to classification (Hanelt, 1992): subg. *Rhizirideum* (G. Don ex Koch) Wendelbo s. l. and subg. *Allium* are roughly light-grained; subg. *Melanocrommyum* is heavy-grained, while subg. *Amerallium* showed small-, medium-, and large-grained sections. Several exceptions from this general rule were also observed. A possible explanation for these differences is a strong correlation of seed size and weight to germination strategy and ecological demands of the species (Hanelt, 1992).

Seed germination behavior and dormancy of more than 90 *Allium* species (about 400 accessions) was tested at different temperatures covering the range between 5° and 26°C (Specht, 1997; Specht and Keller, 1997). The results mainly confirmed temperature related differences for certain species and taxonomic groups (best germination in subg. *Allium* at 11°C-16°C, in rhizomatous groups at 16°C-26°C, but in subg. *Melanocrommyum* at 5°C) as well as to habitat specificity reported in some literature.

The germination experiments also provided data on polyembryony (development of two or more seedlings from a single seed; Specht et al., 2001). Most species with multiple seedlings were found among rhizomatous species with a frequency ranging from 0.075 to 32%. High frequencies of polyembryony are restricted to a few polyploid taxa (*A. splendens* Willd., *A. strictum* Schrad., *A. oreoprasum* Schrenk, *A. lineare* L.).

Seed material of 117 *Allium* species from the Gatersleben collection were used to study the morphology of seedlings (Druselmann, 1992). In this genus the cotyledon consists of a closed sheathing base and a cylindrical upper leaf part with a suctorial tip enclosed in the seed. The disc-like primary seedling axis consists of hypocotyl, cotyledonary node, and epicotyl. The radicle arises exogenously, but all following roots endogenously. If the upper leaf part is much longer than the sheathing base, epigeal germination occurs; in the case of nearly equal lengths, hypogeal germination. About 80% of the investigated species showed epigeal germination and belong to the *A. cepa*-type. The *A. karataviense*-type (present only in subg. *Melanocrommyum*) is also epigeal but differs from the former type the extremely short base of the cotyledon and extremely long upper leaf part. The *A. victorialis*-type and the *A. ursinum*-type show hypogeal germination. The latter differs by a special structure of the epicotyledonary leaf.

Developmental stages of leaf blades and inflorescences were used to establish a phenological classification of the large variability in annual life cycles present in the genus *Allium* (Pistrick, 1992). Different timing of foliage dormancy (summer to winter, winter to spring, winter, or lacking) correlates to taxonomic and phylogenetic aspects. The great majority of species present in the living Gatersleben collections were analyzed in subsequent years. Graphic phenograms were developed which use different signatures for phenophases and phenological events, allowing easier comparisons. Many data on phenology are still awaiting publication.

Comparative studies on ontogenetical flower development dealt only with a few species. They demonstrated the occurrence of obdiplostemony in *Allium* (Pistrick et al., 2001).

Sculptures of the seed testa were studied in a broad array of *Allium* taxa and those of closely related genera. An extreme diversity has generally been found at the species level, and there is also much infraspecific diversity (Kruse, 1984, 1986, 1988, 1992b, 1994). For example, rather simple structures like smooth to indistinctly granulate surfaces were present in sects. *Anguinum* D. Don ex Koch, *Porphyroprason* Ekberg, and subg. *Caloscordum* (Herb.) R.M. Fritsch. Many other groups show periclinal cell walls consisting of a distinct central field, often convex and with verrucate sculptures, and a peripheral anticlinal field. These are regarded as derived characters. Finely (sect. *Tenuissima* (Tzag.) Hanelt) to coarsely (sect. *Allium*, subg. *Melanocrommyum*) undulated anticlinal walls are derived structures as well. More than 20 different types were recognized (Kruse in Fritsch, 1996a), some of which show taxonomic relevance.

ANATOMY AND EMBRYOLOGY

Anatomical analyses of leaf, scape and root structure were extended into nearly all subspecies and species available in the living collection. Although not yet completely finished and published, the results strongly supported earlier conclusions (Fritsch, 1988, 1992b, c, 1993a) that special character states and/or combinations occur in different groups.

Leaves. The presence of only one row of vascular bundles combined with an absence of palisade parenchyma (which causes the sub-epidermal position of laticifers) is a main characteristic of subg. *Amerallium* (the occurrence in *A. parviflorum* Viv., sect. *Brevispatha* Valsecci was erroneously reported; Fritsch, 1996a). One row of vascular bundles combined with the presence of palisade parenchyma and therefore intra-parenchymatic laticifers occur only in sects. *Cyathophora* R.M. Fritsch, *Coleoblastus* Ekberg (Fritsch, 1988) and *Milula* (Prain) Friesen (Friesen et al., 2000). This is probably an ancient character combination (Fritsch, 1988). All other *Allium* groups with flat leaf blades possess two rows of vascular bundles with opposite orientation in the blade part. A regular pair-wise position of opposite vascular bundles in supra- and often also subterranean leaf parts is constantly present in all taxa of subg. *Melanocrommyum* (but not in sect. *Porphyroprason*; Hanelt et al., 1989). In rhizomatous species and members of sect. *Allium* having flat blades, the second (upper side) row originates by multiple divisions and unions of vascular bundles in the basal part of the lamina, and an irregular position (though opposite orientation) of the vascular bundles of the second row develops (Fritsch, 1992c). Position and orientation of vascular bundles continue in cylindrical or semi-terete and fistulose leaf blades as they are in the basal sheath part after having been disturbed only in the transition zone where the sheath opens. Very narrow or thread-like leaf blades are apparently derived structures containing only a few vascular bundles. The majority of *Allium* taxa possess one row of vascular bundles in the sheath part of the leaves, but in subg. *Melanocrommyum* division of vascular bundles and development of a second row begins in the sheath region and sometimes in the region of the bulb (Fritsch, 1992a) independent from the place where the sheath opens and the blade begins.

Scape. The anatomical characters of parenchymatous tissues of the flower scape correspond completely to the principles shown for the leaf blades, but several anatomical characters of sclerenchymatous tissue and vascular bundles support the recognition of six main taxonomic groups in

the genus (Fritsch, 1993a). These roughly correspond to the subgenera accepted in the classification of Hanelt et al. (1992). However, most of these groups were rather heterogenous and could be divided into many subgroups often not corresponding to sections or other taxonomic alliances. The investigation of scape anatomy with a much larger sample of species is an ongoing project.

Roots. Depending on the annual growth rhythm and general life strategies, roots in the genus *Allium* are either annual in bulbous subgenera like *Allium*, *Melanocrommyum*, and some sections of subg. *Amerallium*, or short-lived perennial in rhizomatous groups. Substantial anatomical differences do not exist between them. The number of cell layers, vascular bundles, and the absolute number of cells per tissue is influenced by the distance between base of the root and the analyzed section, by the constitution of the stem from which the root has grown, and by other physiological factors (Fritsch, 1992b). Among the 170 taxa studied, anatomical markers were detected only in a few cases: walls of the cortex cells with knobby thickenings occurred only in sect. *Bromatorrhiza* Ekberg, a many-layered exodermis with strongly thickened cell walls (certainly an adaptation to especially dry growth conditions) is typical for sect. *Campanulata* and a few more rhizomatous species, and strongly thickened outer wall of endodermis cells is only present in subg. *Melanocrommyum*.

Nectaries. Shape, position, and excretory canals of septal nectaries showed much diversity among more than 160 *Allium* species studied (Fritsch, 1992d). Main differences were the position (in the lower half only, more or less median, or only in the upper half) in the ovary, relative and absolute width and size of the nectaries, as well as form, length, and shape of the mouth of the excretory canals. Also the position of the exit of the canal from the nectary and the location of the opening at the ovary were very variable. Although in some cases group-specific character combinations were detected, there was too much diversity for the selection of reliable taxonomic markers. The study of septal nectaries is continuing.

Ovary. The majority of *Allium* species has two ovules in each of the three locules, which develop into up to six seeds (Hanelt, 1992). Multi-ovulate locules dominate in subg. *Melanocrommyum*, and are also present in subg. *Caloscordum* and sect. *Vvedenskya* Kamelin. Uni-ovulate locules occur in sects. *Bromatorrhiza* and *Anguinum*, and pseudo-uni-ovulate locules (only one of the two ovules develop into a seed) were reported for *A. ursinum* L. (Fig. 2, sect. *Arctoprasum* Kirschl.; Hanelt, 1992). These increased

or reduced ovule numbers are regarded as derived (apomorphic) character states. However, pseudo-uni-ovulate locules were also observed in sect. *Compactoprason* R.M. Fritsch of subg. *Melanocrommyum* (Fritsch, unpubl.)

In the last three decades, comparative embryological analysis has become an important method in plant taxonomy. However, in *Allium* interest focused on the main economic species and rather few wild growing taxa. A recent paper (Ashurmetov et al., 2001) summarized current knowledge and studied the development of male and female embryonic structures of three more xerophilous Middle Asian species of subg. *Allium*, as well as their correlation with flower morphology and bud dimensions. Despite an overall similarity of embryonic processes and structures that underlies the close taxonomic relationship of the species investigated, several differences underlined their taxonomic separation at the species level.

KARYOLOGY

The many species available as living plants were also karyologically analyzed. The chromosomes of about 2000 accessions belonging to ca. 170 species were counted. Most results confirmed data known from the literature: most taxa are diploids with a base number of $x = 8$, while polyploids up to the hexaploid level are common in a few groups. Only subg. *Amerallium* showed $x = 7$ as base number as well as the derived chromosome numbers of $2n = 16, 18$, and 22 . "Classical" karyotypes of carmine-stained chromosomes have been established for more than 100 species. Although some results were presented in taxonomic papers (Fritsch, 2000; Fritsch et al., 1998; Hanelt et al., 1989), most results have not yet been published. They confirm that shape, number and position of satellites as well as position of centromeres are generally useful taxonomic markers in the genus *Allium*. However, our karyotypes differed often remarkably from those given in the literature. This also became evident during the study of 23 diploid species of subg. *Melanocrommyum* (including 14 first reports). In this group symmetrical karyotypes occurred that consist of metacentric and submetacentric chromosomes only. However, contrary to several karyotypes published by other authors, neither clear species-specific nor section-specific karyotypes could be established, and an overall high variability of chromosomal arm length ratios among individual metaphase plates was found (Fritsch and Astanova, 1998). Many karyological data published in the literature need to be re-evaluated by a thorough statistical analysis of larger samples.

Differential staining of chromosome parts (resulting in “banding patterns”) has mainly been applied to economically important groups, probably because this method must be adapted anew to every single species. Ten years ago, the relevant literature was compiled and group-specific banding patterns were demonstrated for several rhizomatous sections (Ohle, 1992). The occurrence of intercalary bands and the degree of reduction of telomeric bands proved to be taxonomically important characters. Only in a few cases could these characters be used to derive phylogenies of rhizomatous *Allium* taxa (Friesen et al., 1997b). Here again, additional data are needed.

CHEMICAL COMPOUNDS

Salt-soluble seed storage proteins of 48 *Allium* accessions were electrophoretically analyzed and resembled those of dicotyledons. Present were 2S, vicilin-like and legumin-like proteins, with subunit molecular weights (MW) between 70.000 and 14.000 (Maaß, 1992). A protein with somewhat less than 50.000 MW occurred only in sect. *Codonoprasum* Reichenb., and a strong unreduced protein with MW 65.000 – 70.000 was characteristic for subg. *Melanocrommyum*. All investigated members of subg. *Amerallium* showed an uniform electrophoretic banding pattern, and the same was true for the specific patterns of the investigated rhizomatous taxa.

Widely differing DNA contents per genome had been reported for *Allium* species in the literature. Therefore, nearly 90 species of our collection have been analyzed (Ohri et al., 1998) confirming a more than three-fold difference between highest values (*A. ursinum*: 65.57 pg 2C DNA/genome) and lowest ones (*A. ledebourianum* Roem et Schult.: 17.80 pg). Although there is massive variation in many taxonomic groups, more ancient groups like subg. *Amerallium*, sect. *Anguinum* and subg. *Melanocrommyum* show generally higher values reaching roughly up to 55 pg compared with rarely more than 32 pg in the most advanced subgenera, *Allium*, *Reticulobulbosa*, and *Cepa*. Sect. *Schoenoprasum* Dumort., with an exceptionally low value of 17-19 pg 2C DNA/genome, belongs to the most advanced groups. This points to a significant loss of DNA during evolution.

Comparison of genome size with phenology also exhibited very wide variation, but without any significant negative correlation with flowering period or direct relation with foliage leaf dormancy (Ohri and Pistrick, 2001). Contrary to the ecological perspective of the nucleotype theory mentioned in this paper, in the genus *Allium* there is no general correlation between evolution of genome size and life strategies in the genus.

Many species of the *Allium* collection were investigated by cooperating scientists from other institutions for their cysteine sulfoxide content and alliinase activity (Keusgen, 1999, 2000). All taxa exhibited a characteristic pattern of cysteine sulfoxides, which significantly differs from that of garlic or onion. Their total amount may be higher than 1% of the fresh weight of bulbs. Similar to garlic, *A. obliquum* L. contains high levels of alliin, but is also rich in isoalliin and methiin. Varieties of *A. ampeloprasum* L. revealed high levels of either alliin or isoalliin. Methiin was reported for all investigated samples and is the leading compound for the investigated Asian species like *A. stipitatum* Regel and *A. jesdianum* Boiss. et Buhse.

Different rhizomatous *Allium* species showed specific arrays of volatile sulphur components (Schulz et al., 2000a). Also hybrid plants of several rhizomatous species with *A. cepa* showed different individual profiles of cysteine sulfoxides compared with the parental species. The aroma profile of a hybrid plant was either closer to the female or male parent, or else intermediate (Schulz et al., 2000b).

MOLECULAR MARKERS

During the last decade, molecular techniques have been applied to a broad array of very different plant groups, and became an essential part of the taxonomic investigations of *Allium* and related genera as well. This was accompanied by the development of a wide spectrum of methods available to study specific problems. The initial steps of isolation and purification of DNA had to be adapted (the frequent presence of polysaccharides may strongly disturb these processes) in order to isolate sufficient amounts of nuclear and chloroplast DNA for analysis.

Suitable restriction enzymes cut DNA at specific nucleotide sequences ("restriction sites"). The resulting variably-sized fragments can be separated by electrophoresis and identified after hybridization with specifically marked DNA-probes. The pattern of identified probes obtained (Restriction Fragment Length Polymorphism "RFLP") may have taxonomic relevance depending on the enzymes used. In the genus *Allium*, this method allows taxonomic conclusions to be drawn at the subgeneric to species levels.

Another molecular technique applies the Polymerase Chain Reaction ("PCR") to DNA isolates to generate random DNA segments (Randomly amplified polymorphic DNA "RAPDs") with a single primer of arbitrary sequence. The products of amplification can be separated by electrophoresis and stained for identification. Different primers can be used, and the differ-

ent banding patterns obtained allow the selection of markers and development of a data matrix of genetic identity or distance statistics.

This technique proved useful in the genus *Allium* at the sectional and species levels. Using chloroplast DNA, the results distinguished clearly two completely separated groups in the "old" section *Molium* G. Don ex Koch (in the broad sense of Regel (1875) and Vvedensky (1935)). One group is closely related to North American species. The other is well-separated from all other subgeneric groups, and has been recognized for some time as subgenus *Melanocronium* (Linne von Berg et al., 1996; Samoylov et al., 1995, "1996" 1997, 1999). Not surprisingly, different species of the rather heterogeneous subgenus *Bromatorrhiza* Ekberg (Samoylov et al., 1999) are related to species from different sections of subg. *Amerallium* (Fritsch, 1996a). Also PCR-RFLP based analyses gave very similar results (Mes et al., 1997). Most recently (Fritsch and Friesen, 2002; Klaas and Friesen, 2002) it became evident that a few species are best placed close to the ancient rhizomatous groups. Thus, the subgenus *Bromatorrhiza* is artificial and has to be abandoned.

Sequence data of non-coding DNA regions represent another independent molecular marker system possessing taxonomic relevance. Deletion or insertion of longer base sequences is usually such a rare event that it can be assumed to identify groups of related species. Presence and/or absence of a deletion and/or an insertion can often be identified as the ancestral or the derived state, and thus allow the determination of the true phylogeny. Analysis of regions with a relatively low rate of DNA sequence mutations allows one to draw conclusions at subgeneric and sectional levels, while more mutable regions can deliver information at subspecific levels.

The internal transcribed spacer (ITS) regions of the nuclear genes coding for ribosomal RNA, and the noncoding regions between the chloroplast *atpB* and *rbcL* genes, have provided taxonomically relevant data at subgeneric, sectional and subsectional levels in the genus *Allium* (presented below). Also several other non-coding regions have been proposed for molecular studies in *Allium* (Mes et al., 1997) but have not yet been used.

Another technique was applied targeting a special sequence found in the satellite region of *Allium cepa* chromosomes (Pich et al., 1996). With fluorescence in situ-hybridization ("FISH:" the coupling of a defined sequence to a fluorescent stain), 26 *Allium* species were tested. Only the available members of sect. *Cepa* (Mill.) Prokh. and the taxonomically uncertain *A. roylei* Stearn emitted clear signals with this technique. Among the morphologically rather diverse species of the recent sect. *Cepa*, only small

differences were observed. The region targeted with FISH is possibly a specific taxonomic marker for members of sect. *Cepa*. Unfortunately it could not be applied to living accessions of *A. rhabdotum* Stearn (from Bhutan) and *A. farctum* Wendelbo (from eastern Afghanistan and Pakistan), both of which have never been present in our collection.

Reviews about the different methods applied in Gatersleben and elsewhere to *Allium* and their main results were recently presented (Bachmann et al., 2001; Fischer and Bachmann, 1998, 2000; Klaas, 1998; Klaas and Friesen, 2002). The resulting new views about the phylogeny of the genus, and some more details, will be given in the next sections dealing with taxonomy and classification at different levels.

TAXONOMY OF INFRAGENERIC GROUPS MOSTLY WITH ECONOMIC IMPORTANCE

The rich living collection with many accessions from type locations was a good basis both to determine the natural relations of variously assigned taxa at different taxonomic levels, and to disentangle nomenclatural problems (Fritsch, 1996a, 1999; Hanelt, 1996b). A large part of such results were included in the "Nomenclator Alliorum" (Gregory et al., 1998). Those dealt with in special publications will be briefly reviewed below.

Nomenclatural decisions had been unavoidable in a few cases. Selection of lectotypes of 31 species belonging to subg. *Melanocrommyum* set a reliable basis for further taxonomic research (Fritsch, 1990a). Proposals to conserve the names *Allium ampeloprasum* L. against *Allium porrum* L. (Hanelt, 1996c) and *A. cristophii* Trautv. against *A. bodeanum* Regel (Fritsch, 1999) were accepted and became valid according to the rules of International Code of Botanical Nomenclature.

Allium oreophilum C. A. Mey. (Fig. 3) was the first of the taxonomically unclear species that the Gatersleben group dealt with (Hanelt et al., 1989). According to the sum of morphological, ecological, phenological, chorological, anatomical, karyological and serological characters, as well as specialities of seed testa and growth form, this taxon is much more closely related to subg. *Melanocrommyum* than to any other *Allium* group though it occupies also a rather isolated position within this subgenus. This result was later confirmed by molecular data.

The well known ornamental *A. rosenbachianum* Regel has been compared with the original description, the type specimen, and with living plants collected at the type location in Tajikistan (Fritsch, 1993b; Fig. 4). The ornamental cultivated under that name differs remarkably from the

true species and also from *A. jesdianum* (Fritsch, 1996a). Because no other valid name was available, the ornamental plant has been newly described as *Allium rosenorum* R.M. Fritsch (Khassanov and Fritsch, 1994; Fig. 5).

Likewise, *A. aflatunense* B. Fedt. is not the correct name for another well-known ornamental species. The true species from the Aflatun valley in Kyrgyzstan belongs to the *A. stipitatum*-alliance (which was confirmed during a visit at the type location, Fig. 6) and is quite different from the identically named garden onion. Therefore, the latter was newly described as *A. hollandicum* R.M. Fritsch (Fritsch, 1993b; Fig. 7). Similarly, the true taxonomic identities of *A. jesdianum*, *A. bakhtiaricum* Regel, and *A. hirtifolium* Boiss. (which is a synonym of *A. stipitatum*) could be ascertained on the basis of living material collected in Iran (Fritsch, 1996b). In that paper, sect. *Megaloprason* Wendelbo was revised for Iran, and a key for determination was given. A paper in German deals with the ornamental “drumstick alliums” belonging to this group (Fritsch, 1995).

In addition to incorrect names for cultivated ornamental alliums, several ornamental selections have received the wrong taxonomic name, and various ornamental hybrids on closer examination have turned out not to be of hybrid origin at all or to have parental species other than claimed by breeders and/or bulb traders. A combination of RAPD and genomic in-situ hybridization (“GISH”, the coupling of a fluorescent stain to specially prepared chromosomal DNA) techniques, confirmed ‘Globemaster’ to be a hybrid of *A. maclearii* Bak. (Fig. 8) and *A. cristophii*. On the other hand, ‘Globus’ has *A. karataviense* Regel and *A. stipitatum* as parental species, rather than *A. cristophii* and *A. giganteum* Regel as had been assumed on morphological grounds (Friesen et al., 1997a). Neither GISH nor RAPD suggested the presence of a second genome in several cultivars. ‘Purple Sensation’ (Fig. 7) is most likely a mutant of *A. hollandicum*, while ‘Mount Everest’, ‘White Giant’ and ‘Mars’ belong to *A. stipitatum*, and ‘Michael H. Hoog’ to *A. rosenorum*.

Joint fieldwork with several botanical institutes in different Asian countries resulted in important additions to the living collections of IPK. Several expeditions took part in areas rarely visited before, and formerly overlooked or insufficiently characterized *Allium* species were added to pre-existing regional inventories. One of the most important goals of these missions was to study living plants at their natural sites in order to become acquainted with the extent of variation in, and the ecological properties of, natural populations. Such data were presented for most sections of subg.

Melanocrommyum (Fritsch, "1996" 1997), in which was discussed the possible relations to western Asia, and, more generally, to Mediterranean *Allium* taxa (Hanelt, 1996b).

Long-lasting cooperation with the Uzbek *Allium*-taxonomist Furkat Khassanov resulted in several joint papers. A first publication (Khassanov and Fritsch, 1994) dealt with subg. *Melanocrommyum* in Middle Asia, presenting taxonomic revisions of the *A. sewerzowii* Regel alliance and descriptions of four new species accompanied by color pictures, as well as a few lecto-typifications. Another paper (Fritsch et al., 1998) presented several new species from different taxonomic groups, and revisions for sect. *Brevidentia* Khassanov & Iengal. and the *A. taeniopetalum* M. Popov & Vved. alliance. A revision of sect. *Regeloprasum* Wendelbo for Middle Asia accepted 14 species and subspecies among which 5 were newly described (Fritsch, 2000). This paper presented a special table to compare and identify all taxa. Another joint paper is in preparation.

Based on observations made during fieldwork and on herbarium specimens, an annotated list for *Allium* in the Mongolian flora (Friesen, 1995) recognized 44 (mostly rhizomatous) *Allium* species. Several of them play an important role in the daily diet of the local people (Sanchir et al., 1989). Another paper (Friesen and Özhatay, 1998) published some results of joint fieldwork with Turkish scientists, and presented a revision and key for determination of Turkish rhizomatous alliums.

Collection and study of *Allium* in several areas of Europe and Asia has always been accomplished in close cooperation with local scientists. Reports of these activities also presented special information about rare and otherwise interesting *Allium* species (Friesen and Pistrick, 1991; Fritsch, 1990b; Fritsch et al., 1993). Another paper (Hammer et al., 1995), dealing only partly with *Allium*, focuses on the technical aspects of recognizing and collecting these plants. It features a map of travel routes and working areas during the *Allium* research missions of 1983 through 1993.

A morphological and chorological revision of sect. *Schoenoprasum* (Friesen, 1996) recognised 4 species in Central Asia – South Siberia, one species each in East Asia (*A. maximowiczii* Regel) and in the western part of the Pyrenean peninsula (*A. schmitzii* P. Coutinho), in addition to *A. schoenoprasum* L., the world's most widely distributed *Allium* species, with 3 subspecies. Two subspecies occur in the Pyrenean peninsula, and the morphologically very diverse subsp. *schoenoprasum* was divided into four informal morphotypes.

In a later paper (Friesen and Blattner, 2000), these informal morphological types could not be confirmed, but a clear geographic differentiation has been found by RAPD analysis. Asian and European subgroups are different; and Scandinavian, southern or eastern European material is separated as well. It was also shown that a combination of phenetic, cladistic, and statistical methods of data analysis resulted in clearer phylogenetic interpretations than each of the methods separately. Exclusion of polyploids enhanced the resolution of dendrograms in *Allium schoenoprasum*.

Another study focused on the tetraploid *A. altynolicum* Friesen that was regarded as a natural hybrid of *A. schoenoprasum* ? *A. ledebourianum* s. str. when described for the first time. For a long time, it was misnamed “tetraploid *A. schoenoprasum*” or *A. ledebourianum* (for the true species see Fig. 9) in botanical collections. A species-specific banding pattern of chromosomes supported this hypothesis, but genomic in situ-hybridisation (“GISH”) did not give clear enough results to prove it (Friesen et al., 1997b).

Allium sect. *Cepa*, to which the economically important common onion belongs in addition to several species and hybrids of more local interest, is a group of special concern at the IPK. The first paper (Hanelt, 1985) set a reliable basis for later studies by revising classical taxonomy, ecology and distribution areas of the wild taxa. Further results were included in a rather condensed but illustrated report on this section presenting many historical, biological and taxonomic details (Hanelt, 1990). A broader area of interests was covered by later papers that added short overviews on recent advances in the phylogeny and classification of the genus, and also reported on other cultivated or otherwise exploited *Allium* species of regional to local importance (Hanelt, 1991, 1994, 1995). The updated version of Hanelt’s first report (Fritsch and Friesen, 2002) included information about classification, evolution, and domestication, as well as information about the cultivated species treated in “Mansfeld’s Encyclopedia ...” (Hanelt, 2001).

Application of RAPD and GISH techniques (Friesen and Klaas, 1998) as well as microsatellite (multiple repeats of short base sequences) patterns (Fischer and Bachmann, 2000) confirmed shallots to be so closely related to *A. cepa* that both must be regarded as belonging to one botanical species. GISH only confirmed the close relatedness of the French grey shallot ‘Griselle’ to *A. oschaninii* O. Fedt. rather than to the common onion. However, distribution of microsatellite loci showed alleles similar in size to those of *A. cepa* (Fischer and Bachmann, 2000), lending support to the view that this cultivar is possibly a hybrid of these two species, as originally suggested by morphological and isozyme data (Maaß, 1996a).

Morphologically, *A. oschaninii* (Fig. 10) is closest to *A. cepa*, but RAPD data showed a greater genetic distance between these species than between *A. cepa* and *A. vavilovii* Vved. (Fig. 11) and *A. asarense* R.M. Fritsch et Martin (Fig. 12) (Friesen and Klaas, 1998). Sequences of ITS and *rbcl-atpB* regions (Fritsch et al., 2001) gave identical results. This makes *A. oschaninii* a very improbable wild ancestor of the common onion.

These results and recognition of *A. asarense* as a new wild taxon (from the Elburz range of Iran; Fritsch et al., 2001) may support the hypothesis that *A. cepa* was likely domesticated in south or southwest Asia, rather than inside the more northerly area of distribution for *A. oschaninii*. Perhaps another wild relative (or even the true progenitor of the common onion) might be still alive in a very restricted area of southern or southwestern Asia somewhere south of 40° latitude.

Molecular markers have added more facts about the domestication of Welsh onion *A. fistulosum* L. Although the wild species *A. altaicum* Pall. shows great morphological, karyological and genetic similarity, and highly



Fig. 1. Field area of the *Allium* collection at the IPK.



Fig. 3. *Allium oreophilum* C. A. Mey. (sect. *Porphyroprason*) is widely distributed from Caucasus to East Turkey and South Siberia occupying alpine rubble slopes. This highly ornamental and variable species is much grown in rock gardens (Chatkal Mts. south of Tashkent, Uzbekistan).



Fig. 2. *Allium ursinum* L. (sect. *Arctoprasum*) grows at shady sites in temperate Europe and is sometimes used as a surrogate for garlic. In spite of its decorative flowers it is not much liked in gardens because it tends to become invasive and emits unpleasant smell when the leaves are withering (near Olomouc, Czechia).

fertile hybrids occur between these species, different hypotheses were proposed excluding *A. altaicum* as a possible direct ancestor of *A. fistulosum*. The rich material of both species available at IPK was analysed by PCR-RFLP of noncoding chloroplast DNA, by RAPD of nuclear DNA, and sequencing of the chloroplast *psaA* – *trnS* intergenic spacer (Friesen et al., 1999). The results suggested a monophyletic origin of all accessions of Welsh onion investigated from an *A. altaicum* progenitor. This was basal to many other *A. altaicum* accessions as well, making this species paraphyletic.

The hybrid nature of several vegetatively propagated onion-like alliums was confirmed by isoenzyme analyses (Maaß, 1997a, b) and by application of RAPD and GISH techniques (Friesen and Klaas, 1998), although not all parental species could be determined.

Experiments on the hybridization of *A. cepa* with several rather distantly related species have been conducted by collaborating research groups in other departments of the IPK. With use of embryo rescue and the common onion as maternal parent, hybrid plants of several species combinations



Fig. 4. *Allium rosenbachianum* Regel s. str. (sect. *Megaloprason*) is a botanical species with low ornamental value. It shows rather wide and slightly stalked leaves and smooth scapes (type location near Baljuan, Tajikistan).

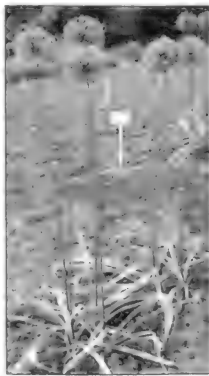


Fig. 5. *Allium rosenorum* R.M. Fritsch ("A. rosenbachianum" of gardens, sect. *Megaloprason*) is a striking decorative species much planted in European gardens. It is characterized by strongly ribbed scapes and narrow leaves. Shown is the cultivar 'Purple King'.



Fig. 6. *Allium aflatunense* B. Fedt. s. str. (sect. *Megaloprason*) is closely related to *A. stipitatum* having also smooth scapes and very wide leaves. It has high ornamental value (Arkit valley, Kyrgyzstan).

All photos from the IPK archives.



Fig. 7. *Allium hollandicum* R.M. Fritsch ("A. aflatunense" of gardens, sect. *Megaloprasum*) is of smaller stature as the true species and has slightly ribbed scapes. Shown is the well known cultivar 'Purple Sensation'.



Fig. 8. *Allium macleeanii* Bak. (sect. *Compactoprasum*) from montane areas in Southwest and Middle Asia is not rarely grown in European gardens as an ornamental. Shown is the broad-leaved variant (syn. *A. elatum* Regel; Darvaz Mts., Tajikistan).



Fig. 9. *Allium ledebourianum* Roem. et Schult. (sect. *Schoenoprasum*) is a large species with conspicuous lilac flowers from South Siberia. In gardens it may cross with closely related species (Altaj Mts., Siberia).



Fig. 10. *Allium oschaninii* O. Fedt. (sect. *Cepa*) occupies stony slopes and rock terraces in Middle Asia. Although very similar to common onion, it is not its closest relative (Bot. Garden Dushanbe).



Fig. 11. *Allium vavilovii* M. Popov et Vved. (sect. *Cepa*) is a rare and endangered species possessing not-inflated, sickle-shaped leaves. It is the closest known relative of common onion but not its direct progenitor (Kopetdag Mts. near Ashgabat, Turkmenia).



Fig. 12. *Allium asarense* R.M. Fritsch et Matin (sect. *Cepa*) was newly described from Iran. This yellowish-green, translucent flowers are an unique feature in this section (Karaj valley, Iran).



Fig. 13. *Allium lusitanicum* Lam. (syn. *A. senescens* L. subsp. *montanum*, sect. *Rhizirideum* s. str.) occurs naturally at dry slopes in many parts of Europe and is sometimes grown in gardens (French Pyrenees).



Fig. 14. *Allium sativum* L. (sect. *Allium*) garlic includes also freely flowering (but seed-sterile) landraces not rare in Middle Asia (garden near Kayrakkum, Tajikistan).

were obtained. Most of them showed a remarkable similarity to the pollen parent. Though their hybrid state could sometimes be deduced from morphological characters, clear differences in parental karyotypes allowed the verification of hybridity. A few disputable cases were solved by applying flow cytometry of DNA contents, GISH, isozyme markers, or the molecular RAPD technique (Keller, 1994; Keller et al., 1994, 1996).

There was a long tradition in Europe of regarding the European representatives of the *Allium senescens* L. group as conspecific with their South Siberian relatives, or as subspecies *A. senescens* subsp. *montanum* (Fries) Holub. Study of karyology and RAPD markers of the rich living collection at Gatersleben (Friesen and Herrmann, 1998) showed great distance from the Asian members and the existence of several well-delimited species in both regions. In Europe, two species were accepted beside *A. angulosum* L.: the ancient segregate species *A. incensiodorum* Radic from Croatia, and *A. lusitanium* Lam. (Fig. 13), which is distributed over large parts of Europe and includes several informal geographic subgroups.

The Gatersleben garlic collection has been investigated using isozymes and RAPD markers. Within this world-wide cultivated and rather variable species, four main groups have been circumscribed (Maaß, 1994, 1996b, Maaß and Klaas, 1995), characterized by morphology as well as geographic origin. This geographic differentiation is apparently connected with different climatic adaptations of the groups, and does not reflect the geographic area where they evolved. Several morphological characters (pseudostem shape, inflorescence formation, and bulb structures) correspond more or less closely to these groups (Keller and Senula 1999, 2001; Senula and Keller, 2000).

Among these groups, the most heterogeneous one includes most types traditionally called *A. longicuspis* Regel, characterized by long filaments exerted up to 2 mm above the tip of the tepals. However, such long filaments were also found in all other groups if the bulbils were removed at an early stage of development (Maaß, 1996b). Thus, long anthers are not a suitable character to separate species, and all the different forms of true garlic belong to different cultivar groups of one botanical species, *Allium sativum* L. (Fig. 14).

During the last decades, *Allium* taxa have become popular ornamentals, especially for spring and summer bloom. They are sold as bulbs that are commercially produced mostly in the Netherlands. A recent review (Kamenetsky and Fritsch, 2002) presents short biological, horticultural, and taxonomic characterizations of about 75 species and 30 cultivars. The taxonomically dif-

ficult sect. *Megaloprason*, to which most of the ornamental “drumstick alliums” belongs, has been dealt with in more detail in earlier papers (Fritsch, 1995, 1996a). Another review briefly characterized about 85 *Allium* species from Central Asia having ornamental properties (Fritsch, 1997).

CONCLUSIONS FOR GENERAL TAXONOMY AND CLASSIFICATION OF *ALLIUM*

The permanent study of a broad array of living *Allium* species belonging to all subgenera and many sections, in nature as well as under cultivation over many years, resulted in recognition of an astonishing diversity of morphological and phenological characters and character states not visible in herbarium specimens. These data caused intensive discussions about possible relations of taxa and their affiliations to taxonomic groups. The results of other investigations that often led to different and sometimes controversial conclusions, and the many substantially different points of view and proposals for classification published in the literature, were considered as well. All these results have been condensed into the “Gatersleben infrageneric classification proposal” published in 1992 (Hanelt et al., 1992). It became our “milestone” mark at the beginning of molecular era in *Allium* taxonomy and classification, and has remained the measure for comparison for our more recent results. Formal description and nomenclatural validation of the newly proposed sections and subgenera were given in a separate paper (Hanelt and Fritsch, 1994). Somewhat later, re-classification of some groups was also discussed in more detail (Fritsch, 1996a).

Because of many newly described species and subspecies, as well as availability of new data from many sources, a more detailed classification was proposed for subg. *Melanocrommyum* that finally accepted 16 sections and 19 subsections (Fritsch, 1992a, 1993b, 1996a, Khassanov and Fritsch, 1994). However, there remained some difficulties for the recognition of some of these groups because a few morphological characters were transitional. PCR-RFLP studies of cpDNA of about 40 species from different geographic regions (Mes et al., 1999) detected very complicated relationships, perhaps best explained by gene flow between species. The group has apparently undergone a rapid and recent evolutionary radiation in the strongly arid region from the Near and Middle East to Central Asia. The youngest geographic center of diversity is in the border region of Tajikistan, Uzbekistan, Afghanistan, and Kyrgyzstan. This reticulately evolved [Ed. note: hybrid speciation] diversity cannot adequately be classified by means of traditional hierarchical systems. Thus currently a natural classification cannot be presented for subg. *Melanocrommyum*.

Other species analyzed by PCR-RFLP of cpDNA presented strong arguments for some substantial changes in *Allium* generic classification (Mes et al., 1997); e.g., the subgenera *Rhizirideum* and *Bromatorrhiza* are probably highly artificial groups, and acceptance of *Nectaroscordum* Lindl. as a genus makes *Allium* paraphyletic.

Sequence data mainly of the ITS region were especially helpful in finding the natural relations of taxa controversially placed in earlier classifications inside or outside of *Allium*. Recent data (Friesen, in prep., Fritsch and Friesen, 2002; Klaas and Friesen, 2002) strongly support recognition of three distinct evolutionary lines, all of which are represented by ancient as well as advanced groups (Fig. 15). Among the most unexpected conclusions were the incorporation of such morphologically well separated taxa as *Nectaroscordum* and *Milula* Prain into a monophyletic genus *Allium*, and the exclusion of species of *Nothoscordum* Kunth. that are morphologically very similar to *Allium*. Contrary to former views, rhizomatous *Allium* species are neither a monophyletic group nor the most primitive of the onions. Subgenus *Amerallium* is a monophyletic unit comprising rhizomatous as well as bulbous species, and the rhizomatous sect. *Anguinum* is much more closely related to the exclusively bulbous subg. *Melanocrommyum* than to any other *Allium* group. Additionally, the insertion of subg. *Allium* among the most advanced rhizomatous groups conflicts with traditional classifications.

As a consequence, the huge number of characters and character states reported for *Allium*, *Milula* and *Nectaroscordum* (e.g., the well-known diversity of rhizome shape), must be given some new and wider interpretation. This involves characters formerly regarded as being exceptional or without

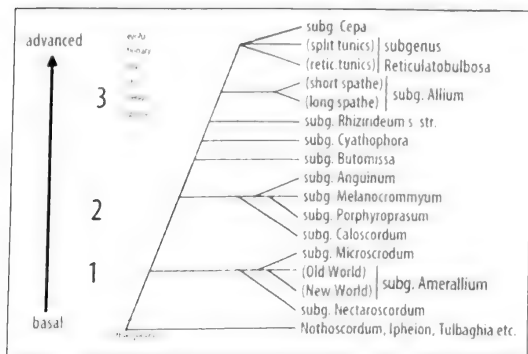


Fig. 15. Proposal for a phylogenetic classification of *Allium* according to ITS sequences (Friesen, in prep; new names still unpublished).

relevance to classification purposes. Likewise, some traditional views must be revised. For example, true bulbs (composed of 1-2 strongly thickened bladeless prophylls) are a not derived character as formerly generally accepted (e.g. Hanelt et al., 1992), but an ancestral one in *Allium*, whereas false bulbs

(composed of thickened prophylls plus thickened basal parts of complete leaves) and the development of rhizomes have been derived more than once.

One conspicuous feature of our ITS data is the unusually large infrageneric genetic distances within *Allium* expressed by Kimura distances above 40% (Friesen, in prep). In other plant families, infrageneric distances are mostly less than 10%. These results point to a very ancient origin of *Allium*, though the degree of molecular evolution was not accompanied by a comparable rise in the number of taxonomic categories recognized in the genus.

The results generally agree rather well with the subgeneric classification proposed in 1992 (Hanelt et al., 1992), with the addition of some new sections proposed somewhat later (Khassanov and Fritsch, 1994). Although several groups must be recognized at a different taxonomic rank, there is scarcely any need to create new names. ITS data confirm the separate position of sects. *Schoenoprasum*, *Campanulata* Kamelin, *Codonoprasum* F. Herm., *Oreiprasum*, and *Vvedenskya*. This is also true for sects. *Cepa*, *Anguinum*, *Butomissa* (Salisb.) Kamelin, *Reticulobulbosa* Kamelin, *Allium*, and *Scorodon* Koch in the narrow sense. This is independent from the fact that they became or remained the name-bearing components of subgenera to which other sections may be affiliated. Surprisingly, most small sections separated recently from sects. *Allium* s. lat. and *Scorodon* s. lat. (Khassanov, "1996" 1997) have been confirmed by molecular data, but the alternative mode to subdivide sect. *Allium* s. lat. by Mathew (1996) has received no molecular support. The sections *Cyathophora* and *Coleoblastus* will be positioned basally to most groups of former subg. *Rhizirideum* (in the broad sense). Along with sect. (former genus) *Milula* and a few previously misplaced species, they present an ancestral alliance in *Allium*.

The mathematical methods applied to molecular analyses are influenced by the number of species of different groups, or accessions of one taxon, that can be incorporated. Modern computers allow analyses of large data sets of two hundred or more taxa. This turned out to be sufficient in most cases. However, the presence or absence of taxa (and even of genetically different individuals the same taxon) may strongly influence the result. The availability of the living collection in many cases allowed the testing of the stability of the resulting dendrograms or cladograms. Either different accessions of the same taxon, or closely related species, could be exchanged against other ones. If such exchanges did not substantially influence the resulting dendrograms or cladograms, they were accepted. Many of the results obtained during the course of these investigations are still awaiting publication.

An adequate classification of the astonishing and phylogenetically complicated diversity of the genus *Allium* (as circumscribed in Fig. 15) will require the acceptance of no less than 50 infrageneric groups at the subgeneric, sectional, and subsectional levels. This is an inconveniently high number, with the result that dealing with *Allium* may necessitate time-consuming and occasionally frustrating navigation through long keys and extended comparisons of characters.

Is there an easy way to reduce these problems? We calculated that alternative ranking of some groups will scarcely reduce the amount of work involved, but this remains open to further discussion. We also calculated whether the division of *Allium* into several smaller genera, as has been sometimes proposed, could result in a more manageable classification. However, the results were shocking; more than 30 generic names described between 1754 and 1869 that refer to *Allium* species would have to be precisely examined according to the current rules of botanical nomenclature. Several of them would have to be revived; perhaps a few new ones would have to be created. Moreover, about 400 new species names would have to be combined because the current subgenus *Allium*, which would remain unaltered, includes about 300 species. Ultimately, the same problem would only be shifted to other taxonomic levels, yet hundreds of new binominals and resulting new synonyms would have to be recognized. This is why the IPK taxonomists strongly oppose this approach.

Towards the final years of the last millennium, research activities of the IPK Taxonomy Dept. moved on to other plant species, and *Allium* became one of the less important research targets. Currently the living *Allium* accessions are part of the IPK Genebank collections under the name of "*Allium* reference collection". It is still under the taxonomic supervision of Taxonomy Dept. (see also <http://www.ipk-gatersleben.de/en/departement/taxonomy/index.html>), and it remains accessible for visitors. A restricted seed exchange with scientific institutions is maintained.

Color pictures of recently described *Allium* taxa are available in the internet under <http://www.mansfeld.ipk-gatersleben.de/>, and more images of species and other data will be added in near future.

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A NONDESTRUCTIVE HARVESTING TECHNIQUE FOR THE COLLECTION OF NATIVE GEOPHYTE PLANT SPECIES

Mark P. Bridgen

Cornell University, Long Island
Horticultural Research & Extension Center
3059 Sound Ave., Riverhead, NY 11901
Telephone: 631-727-3595, Fax: 631-727-3611
E-mail: mpb27@cornell.edu

INTRODUCTION

During the past decade there has been a growing awareness of the dangers of over-collecting wild bulbous plants for the horticultural trade. Unscrupulous collectors and unwitting purchasers of bulbs allow thousands of the world's rarest bulb species to be harvested from their wild habitats. This has resulted in the placement of certain bulbous plants on the CITES (Convention on International Trade in Endangered Species of Wild Flora and Fauna) list. Fortunately, efforts are being made to propagate geophytes through sexual and vegetative means (Bircher et al., 1998).

In addition to over-collecting, growing demographic pressures and diverse anthropogenic menaces such as the growth of agricultural and urban areas, overgrazing, overuse of natural resources, erosion, and man-made fires have threatened valuable plant species. Local residents in countries with native geophytes also unwittingly endanger plants when they dig up bulbs and cut flowers for commercial purposes. Certain plants, such as those in the Amaryllidaceae, are in greater danger from these man-made problems because of specific characteristics of their biology. Many of the amaryllids have long generation times, incompatibility factors, disease susceptibility, and specialized cultural needs. In order to insure the future of wild species, programs are needed to educate those who do not realize that their practices are harmful. In addition, new procedures and techniques need to be developed and implemented so that native geophytes can be harvested in a non-destructive manner.

To avoid the dangers of damage or extinction from collecting bulbs from the wild, conservation-through-cultivation initiatives (Cunningham, 1988), or the commercial production or "farming" of bulbs is an alternative. There are several advantages to the conversion to commercial agriculture: (1) It will lead to the controlled propagation of species in nurseries and green-

houses. Long-term survival of plants under cultivation will reduce pressures on wild stocks. (2) Commercially propagated plants can have their origin labeled at sale on all transit, trade and health documents. This process will help to make a distinction between commercially grown plants and those that are collected from the wild. The consumer will know the difference and hopefully this difference will affect their decision to purchase. (3) The threat of introducing unknown diseases or pests via wild plants will be reduced or eliminated. (4) High quality and healthy plants will be available for international trade. Plant health certificates, or phytosanitary certificates, will be easier to obtain for those who sell plants to other countries. (5) Commercially produced plants are easier to establish than those bulbs that are removed from their native environment. (6) The plants will not be subjected to an abrupt break in their growing period and can be expected to flower at a predictable time. (7) Native species and their habitats will not be damaged from collection in the wild. (8) Cultivation ensures a renewable, reliable supply of stock plants. (9) The collection of plants in the wild can be quick and inexpensive, but commercial production is even less expensive by saving on time and travel expenses. Plant micropropagation techniques can make commercial propagation much less expensive. (10) Collections of plants can easily be used for breeding and new plant development (Lu and Bridgen, 1997).

Although the collection of native geophyte species can endanger their survival, it is also true that the collection of native plant species is critical to the hybridization and development of novel plants. As world bulb trade issues are resolved, the phasing out of wild-source material for breeding may occur.

Since 1988, when I made my first trip to Chile, I have been attracted by the beauty and diversity of Chilean geophytes. Chile's unique environment for bulbs, corms and rhizomes is a result of the geographical barriers that isolate it from the rest of South America. The Pacific Ocean to the west and south, the Atacama Desert to the north, and the Andes Mountains to the east allow Chile to have some 5200 species of flora arranged in 1035 genera and 200 families with 50% being endemic. The petaloid geophytes have approximately 180 species with almost 90% endemic (Hoffmann, 1989). However, as there are a substantial number of endemic geophytes in Chile that are at risk of extinction, conservation measures and nondestructive harvesting techniques need to be implemented to save these endangered species.

Plant tissue culture techniques such as embryo culture (Bridgen, 1994a), micropropagation (Lu et al., 1995; Chiari and Bridgen, 2000), somatic embryogenesis, and mutation breeding (Bridgen, 1994b) have been used to facilitate classical breeding and to enhance commercial plant propagation. Embryo culture procedures have been especially valuable to research programs with *Alstroemeria* and other Chilean geophytes (Bridgen, M.P. 1994b; Bridgen 1997). Embryo rescue is useful because many interspecific crosses fail to produce viable seed and progeny *ex vitro*. This can be attributed to one of several reasons: the embryo may not develop fully, the endosperms may fail to form properly, or the embryo aborts before maturity. By removing immature embryos from the ovule and placing them on a sterile, nutrient medium *in vitro*, the embryos can survive and grow. Embryo culture can also be used to release embryos from dormancy requirements because immature embryos will often readily germinate *in vitro*. This bypass of the dormancy requirements also shortens the growing time of the plants.

The success with Chilean geophytes in our laboratory has led us to propose *in vitro* techniques as a nondestructive harvesting technique for the collection of native geophyte plant species. After the plant parts are collected and successfully cultured *in vitro*, they can be used for a variety of purposes (Preuss, 1999).

BACKGROUND

Plant tissue culture is also referred to as micropropagation, plant cell culture, plant organ culture, plant culture, *in vitro* plant culture, or test tube culture. Plant tissue culture is a very popular area of biotechnology and plant physiology that can be used for several purposes including, but not limited to micropropagation, the rapid propagation of plants, the elimination of viruses and diseases from plants, haploid plant production, protoplast isolation and utilization, embryo culture, production of botanical substances, genetic engineering, cell mutation and selection, synthetic seed production and studies in fundamental plant anatomy, development, nutrition and physiology. Simply stated, plant tissue culture is the growth of plants under controlled environmental conditions on sterile nutrient media.

Plant tissue culture techniques are best completed under clean conditions such as a clean box or laminar air flow hood in a laboratory. However, it has been demonstrated in several situations that the aseptic culture of plants can be accomplished under less-than-sterile conditions. This observation led to the development of the following protocol.

PREPARATION

The first step in this procedure is to plan and prepare before leaving to collect. Although the technique is simple, preparation is needed. Supplies need to be ordered, media need to be made, and tools such as forceps and scalpels with new blades need to be gathered.

Sterile, polystyrene Petri dishes, 60 mm x 15 mm in size, can be purchased (Falcon Disposable Petri Dishes #351007, Becton Dickinson Labware, Franklin Lakes, NJ 07417-1886) for use with this procedure. Larger Petri plates can also be used, but the smaller sizes are easier to transport in luggage. Glass Petri dishes should not be used because of the potential for breakage. Basic 25% Murashige and Skoog medium (Murashige and Skoog, 1962) with 25% sugar concentration is usually sufficient to supply nutrients and carbohydrates to the plant material, but is not so high in salt content to cause a water potential problem. No growth regulators need to be added to this medium. Due to the lack of research with many of the unique plant species, it is uncertain what the effect the growth regulators may have on the plants. Once the plants have been collected and returned to their new home, they can be subcultured onto more appropriate media under clean conditions.

Media need to be prepared in advance of departure. By making the media at least four or five days in advance, it can be inspected for contamination. Any dishes that are contaminated should be discarded. Also, the media should be allowed to set under a running laminar air flow hood at least eight hours after autoclaving to allow time for it to dry out slightly. Drying can continue for up to 24 hours depending on the quantity of medium in the Petri dishes. Do not allow desiccation and drying of the medium to occur. Once the medium is free from condensate, place the original sterile plastic sleeve back over the Petri dishes. Seal the sleeve shut at the opening with tape to prevent the entrance of contaminants.

Other supplies that need to be collected include 95% ethanol in a sealed container that is small enough to transport easily, but large enough to hold approximately 100-250 ml. The ethanol will be used to sterilize the forceps, scalpels, and plant material. Strips of Parafilm (Parafilm "M", American Can Co., Dixie/Marathon, Greenwich, CT 06830) should also be prepared and will be used to wrap the Petri plates once the plant material is cultured. Small, fine-tipped forceps and scalpels should also be included in this inventory. They will be used for the actual removal of embryos or ovules. A box of new plastic garbage bags should be taken along and will be used as the sterile work place at the collection site. Large, 10 cm x 2 cm, disposable Petri

dishes need to be included in the supplies and will be used as the work surface when dissecting plant material. Glass Petri plates, although easily breakable, can also be used as an alternative to the disposable dishes, because the glass can be flame sterilized.

Other typical plant-collecting supplies such as permanent markers for labeling, various sized paper bags and cellophane envelopes for storage of collected items, hand pick for digging, GPS (Global Positioning System) for identifying exact location (latitude, longitude, elevation), matches, and tape should also be gathered.

Airport security measures need to be considered when packing some of the items listed above. Although 95% ethanol (ethyl alcohol) is as flammable as some of the commercial alcohols that are allowed to be carried on flights, it should be stored correctly in checked luggage. Sharp items such as scalpels, picks, and forceps cannot be placed in carry-on luggage.

PROCEDURES

One of the reasons that monocotyledonous geophytes are in danger when they are collected is that their anatomy does not allow for successful stem cuttings to be removed or other nondestructive vegetative harvesting techniques to be used. Therefore, the bulbs or other underground storage organs need to be dug and removed. To avoid this destructive harvesting procedure, ripe or dry seed pods can be detached from the plants, sterilized, and tissue cultured. This procedure prevents destruction of the mother plant and allows easy international transport.

Ideally, the seed pods should be full and close to maturity but the seeds should not have dehisced. The larger the ovary, the older the embryos will be, and the greater the chance of success. However, one of the advantages to this technique is that the tissue culture procedure allows even very immature seeds to survive and grow under most situations. Examine the outside of the ovary or seed pod very carefully. The ovary should not be split open because the seeds that are inside will not be able to be sterilized. The seed pod should also not be damaged or punctured; this is a possible sign that an insect has visited and may have laid eggs inside. In addition to being difficult to sterilize, collectors do not want to be responsible for introducing a new pest to their country.

If possible, seed pods should be gathered and stored in a cool, dry location during the day while collections are being made. At the end of the day, when collectors have returned to their camp, motel, or other habitation, they can perform the following procedures to the collected materials.

First, identify and prepare a clean work area. Ideally, this location should be indoors or protected from wind. The less air circulation, the better is the site. Remove the seed pods from the collected material making sure that the pods are as clean as possible; remove excess leaves or other debris surrounding the ovary. Set up the work area, plan the procedure, and gather all of the necessary items. A planned process will decrease the chance of contamination.

Hands and arms should be well scrubbed with soap and water and subsequently cleaned with 95% ethanol. Open one of the new, sterile garbage bags to be used as the sterile work surface. All of the necessary tools should be placed inside the bag: forceps, scalpels, media, Petri plates, ethanol, and pods. Place an ovary or two in the ethanol for several seconds to minutes. As long as the seed pods are completely sealed, the seeds will not be damaged. Place the forceps and scalpels in the ethanol to sterilize them. Remove the ovaries with a sterile forceps, one at a time, and hold them for 30-60 seconds to allow the ethanol to evaporate.

At this point, one of two procedures can be used. Either the entire, sterile ovary can be cultured, or it can be cut open aseptically to remove the ovules and embryos. Smaller ovaries can be sterilized and immediately cultured. Then later, when the plant material is in a cleaner location, they can be aseptically cut open under a laminar air flow hood and have the embryos excised. Large ovaries such as those produced by some of the *Amaryllidaceae* and *Alstroemeriaceae*, are sometimes too big to fit inside a Petri dish. They will need to be aseptically opened and have the ovules removed. Remember that the ovules and embryos that are inside the ovary are sterile if the ovary has not opened or been damaged. Once the ovary is open, only sterile forceps or scalpels should be used for all manipulations. While the Petri dish is open and the medium is exposed, all movements should be made quickly with as little air movement as possible.

Once the ovaries, ovules or embryos are cultured, they should be sealed and the plates wrapped with Parafilm. The wrapping will prevent contamination from entering, as well as from exiting. The accession numbers for each collection should be written directly on the plate with a permanent marker. This process can be repeated for all of the plant material. As sterile Petri plates or sterile work surfaces are exhausted, new work surfaces can be prepared by wiping with 95% ethanol. The forceps, scalpels, and work surfaces should be repeatedly sterilized between accessions. When the plates are full, they can be reinserted into the sterile plastic sleeve and taped shut.

As with whole-plant collecting, it is important to keep good records. A diary or logbook should be used to enter accessions. Entries should be made in pencil and backup copies should be made as time permits. Each accession should be recorded with botanical and common names of the plant if known, GPS reading (elevation, latitude, longitude), location, date, and notations about the soil type (sandy, clay, etc.) and other vegetation that is near. Sound record-keeping methods assist in the quality and enjoyment of plant collecting and also assists with the productive exchange of plants. Computer spreadsheets are very useful to log accessions alphabetically by genus. The spreadsheets can accommodate a variety of useful information such as propagation records (dates, methods, success rates, etc.), records of people who obtained the plant material, garden performance, photographs taken, etc. (Hannon, 1997).

CONCLUSION

We have tested the described procedures during four different plant-collecting trips to Chile under different environmental conditions. Species of *Rhodophiala* (Fig. 1), *Conanthera* (Fig. 2), *Alstroemeria* (Fig. 3), *Leucocoryne* (Fig. 4), *Leontochir*, *Pasithea*, and *Zephyra* have been collected by using this technique. On average, contamination rates from these procedures are less than 20% -30%. Germination of the cultured ovules and growth of cultured embryos is as high as 90%, but can be unsuccessful depending on the species and conditions. Overall, success rates have averaged from 70%-90% (Fig. 5).

Depending on the final destination of the *in vitro*-harvested plants, proper plant import permits need to be obtained before leaving the home country. Although this high-tech procedure allows the transport of sterile plant parts, they are still considered agricultural materials.

Although the overcollection of plants for the horticultural market has threatened the survival of some plant species, and although global conservation efforts and law enforcement is difficult, there is hope! By using novel techniques such as the one described, the over-exploitation of indigenous plants can be reduced or eliminated.



Fig. 1. *Rhodophiala bagnoldii* from the Atacama Desert in Chile.



Fig. 2. Chilean geophyte, *Conanthera trimaculata*.



Fig. 3. *Alstroemeria werdemannii* growing in the sandy soils of the Atacama Desert, Chile.



Fig. 4. The flower of *Leucocoryne coquimbensis*, a bulbous plant found in central Chile. Photo by Alan W. Meerow.

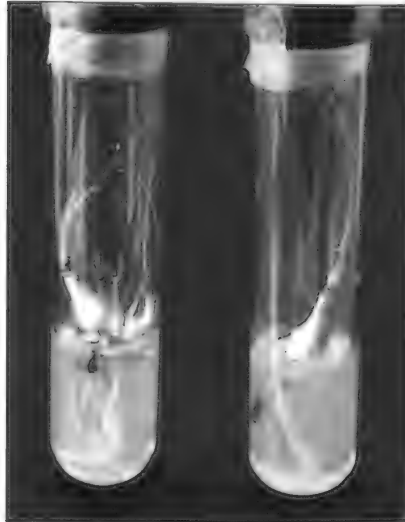


Fig. 5. *In vitro* micropropagation of *Rhodophila* species that were originally collected by nondestructive harvesting technique.

All photographs by Mark Bridgen except where noted.

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**SOUTH AFRICA'S JEWELS OF THE DESERT:
A REAPPRAISAL OF THE GENUS *DAUBENYA* (HYACINTHACEAE)**

John Manning

Compton Herbarium, Private Bag X7, 7735 Claremont, South Africa

There must be few lovers of bulbs who have not heard of, if not actually seen, that extraordinary Cape member of the Hyacinth family, *Daubenia aurea*. Looking for all the world like the discarded peelings of some brilliantly colored citrus fruit, the plants have an exotic, almost bizarre appearance that is in stark contrast to the austerity of the high plateau landscape from which they spring. Rare in nature, the species is restricted to a handful of colonies scattered in a narrow strip along the base of a stony ridge that meanders along the escarpment at the southeast margin of South Africa's interior plateau. From north to south this ridge is no longer than 10 km in length. Nowadays, the location of some of these colonies is well known, and, as they are adjacent to good quality secondary roads, it is not a difficult matter to visit the plants. This was not always the case, however, and the early history of the species is one of mystery and excitement. But no matter how familiar the species might have become, it never fails to excite admiration in all who see it (see "Magnificent *Daubenia*" by John Lavranos & Charles Craib in *Herbertia* 52: 22–25 for a detailed discussion of the species). It certainly succeeded in amazing the British botanist, John Lindley, when he described it in 1835, and he did not hesitate erecting a separate genus just for it.

The genera of Hyacinthaceae are notoriously difficult to define adequately. In practice, this has resulted in the segregation of various groups of closely related species as separate genera by taxonomists. The species of each segregate genus share one or more morphological peculiarities that set them apart. The remaining, less distinct species, have then been relegated to more or less ill-defined genera. Known more picturesquely as *portmanteaux* genera, these botanical catch-alls include *Ornithogalum* and *Scilla*. An alternative, and arguably even less meritorious practice, favoured by some botanists has been to recognise every small group of species within these "catch-all" genera as a separate genus in itself. A proliferation of small or even monotypic genera has been the result, each of which is defined by various minutiae that serve only to obscure more general relationships between these groups of species. An uneasy mix of these two philosophies currently holds

sway within the Hyacinthaceae. The morphological tangles that are strangling the emergence of a meaningful circumscription of genera within the family are only now beginning to give way. The sword that is cleaving this Gordian knot is DNA sequencing. Employed correctly, this technology constitutes a powerful new source of data for analysing the relationships between species without the confusing façade that morphology often throws over the underlying structure. One of the groups within the Hyacinthaceae that is yielding particularly well to this methodology is the alliance of largely South African genera recognised by some workers as the tribe Massonieae. This includes the somewhat confusing assemblage of stemless Cape genera characterised by a pair of prostrate leaves: *Androsiphon*, *Amphisiphon*, *Daubenya*, *Massonia*, *Neobakeria* and *Whiteheadia*.

Epitomising the traditional taxonomic practices that have been employed in the family, the genera *Androsiphon*, *Amphisiphon*, *Daubenya* and *Whiteheadia* were all erected to accommodate single species that differed from their relatives in various attributes of floral morphology. Floral variation within genera of the Hyacinthaceae is on the whole relatively modest, thus where relatively major differences occurred, they were construed to represent sufficient grounds for recognising separate genera. The intellectual climate of the time in botany stressed differences over similarities. For example, in *Androsiphon*, the stamens are fused into a slender tube. This peculiarity also characterises *Amphisiphon* but is accompanied here by a fusion of the tepals. *Daubenya* was characterised by the highly exaggerated outer tepals in the lower flowers, while *Whiteheadia* was recognised by its elongate spike of sessile flowers sheltered beneath a conspicuous crown of sterile bracts. Predictably, the two remaining genera in this alliance, *Massonia* and *Neobakeria*, were less easy to recognise and, in fact, of late are usually combined as one. This is in contrast to earlier workers who reserved the genus *Massonia* for those species with large bracts and very condensed, rounded inflorescences. *Neobakeria* accommodated the remaining few species with smaller bracts and more elongate inflorescences.

Most of these small genera are as rare or even rarer than *Daubenya aurea* itself. Both *Androsiphon* and *Amphisiphon* are known from only two or three populations around the village of Nieuwoudtville in Northern Cape. This small farming settlement lies a little way from the western edge of the Bokkeveld Escarpment, whose sandstone ramparts form the northernmost extension of the Cape Floral Region. Nieuwoudtville, with good reason known locally as the Bulb Capital of the World, lies across three very



Fig. 1. *Daubenia aurea*.



Fig. 2. *Daubenia capensis*.



Fig. 3. *Daubenia namaquensis*.



Fig. 4. *Daubenia stylosa*.

All photographs by John Manning.

Fig. 5. *Massonia jasminiflora*.Fig. 6. *Whiteheadia bifolia*.

dissimilar soils and their associated vegetation types. This geological complexity coincides with a sharp rainfall gradient and relatively open vegetation to provide a diversity of habitats highly suitable for geophytes. Excavation of soil samples in the vicinity has yielded the almost unbelievable total of 25,000 bulbs in a square meter!

Most of the four accepted species of *Neobakeria* are likewise known from small areas. The two most localised are *N. namaquensis*, from the sandy flats east of Springbok in Namaqualand, and the species recognised as *N. burchellii*, which is known from two populations on calcareous coastal sands between Saldanha Bay and Paternoster, just over 100 km north of Cape Town. The two remaining species, *N. comata* and *N. marginata* are more widespread across parts of the southern African interior plateau. In sharp contrast to the highly localised nature of these species, most species of *Massonia* and *Whiteheadia* are relatively widespread across suitable parts of the country. For all six genera this means the winter-rainfall region of southern Africa, particularly the western parts of the interior plateau.

Although the species in all of these genera, with the possible exception of *Massonia* itself, are fairly well understood, the same could not be said until recently about the relationships between them. It seemed likely that *Amphisiphon* and *Androsiphon* were related to one another by virtue of their

unusual, fused stamens. In turn, both were considered to be near *Daubenia*, if only because they were not white or pink in color. Any more exacting relationships between the genera remained unresolved. *Massonia* was usually combined with *Neobakeria* and, in an extension of this, Lavranos & Craib (l.c.) were led to the conclusion that *Daubenia* was 'closely related to *Massonia*, from which it seems to differ only in the dimorphism of its florets...'. Actually, irregular lower flowers are also found in the inflorescences of *Neobakeria namaquensis* and *Massonia comata*, although of a different form than that evident in *Daubenia*. This floral dimorphism is quite marked in *N. namaquensis* and led the German workers, D. & U. Müller-Doblies to restrict the genus to that one species alone, removing the remaining species of *Neobakeria* to the genus *Massonia*. Matters rested uneasily here until the investigation of DNA sequences within the family began to shed some extraordinary light onto the problem.

The least surprising result of these studies was the close relationship that they indicated between *Whiteheadia*, *Massonia* and the genus *Lachenalia*. The large, predominantly winter-rainfall genus *Lachenalia* had long been considered to form part of this alliance, largely on the basis of its smooth, rounded seeds and more or less tubular flowers. The results from DNA sequence analysis were thus merely a vindication of the morphological data. What was quite unexpected, however, were the relationships suggested for the remaining genera in the group. Although there was no doubt that the genera *Amphisiphon*, *Androsiphon*, *Daubenia* and *Neobakeria* were extremely closely related to one another, there was no evidence at all for an anticipated relationship between these genera and the *Massonia*-group. What DNA sequence analysis in fact suggested was that the similarity in the leaves and inflorescence structure of these two groups was an instance of convergence or parallel evolution. Moreover, as often occurs when molecular evidence of phylogenetic relationship is incongruent with morphological data, a closer examination of these characters supported this conclusion. The earlier distinction between the species of *Massonia* with large bracts and the species of *Neobakeria* with small bracts was thus spectacularly vindicated. However, another almost more startling revelation was to emerge. The genetic differences between the species of the *Daubenia*-alliance were so small as not to justify the recognition of more than one genus for the lot! All of the species previously recognised as comprising the four genera *Amphisiphon*, *Androsiphon*, *Daubenia* and *Neobakeria* are most accurately treated as a single genus. Fortunately for us, the oldest name for this group is *Daubenia*. The result of all this molecular genealogy is that

the genus *Daubenyia* has been enlarged to accommodate another six species. With one stroke the genus has thus become the morphologically most diverse in the family in terms of flower form, but retains a striking underlying similarity in the vegetative morphology of these apparently disparate species. All of them share unusual glossy leaves which have the surface marked with longitudinal depressed lines and which fragment at the base into narrow papery strips when they dry. The cause of the startling differences in the flowers of these species has become evident with further study of the species in the wild. They relate to the wide variety of different pollinators to which each of the species is adapted, including honeybees, noctuid moths, monkey beetles, sunbirds and possibly even rodents. Such a diverse spectrum of pollinators is not known in other genera of Hyacinthaceae and is clearly the reason for the unprecedented floral diversity among these species. Botanists, like the pollinating agents that fuelled the process of natural selection, discriminated between the species. While this was a matter of survival for the animals concerned, it merely resulted in a great deal of intellectual confusion for the humans!

COMPARISONS BETWEEN THE REPRODUCTIVE FITNESS
OF TWO SPECIES OF *NARCISSUS* L. (AMARYLLIDACEAE)
FROM SOUTHERN SPAIN¹

Harold Koopowitz^{2*}, Bradford A. Hawkins², Hendrik van der Hoven³,
Derrick Donnison-Morgan⁴ and Marilyn Howe⁵

²Ecology and Evolutionary Biology, University of California
Irvine, CA 92697, USA.

³35 Nooitgedacht Dr., Hout Bay, 7800, South Africa.

⁴Apt. de Correos 137, 03820 Cocentaina (Alicante), Spain.

⁵P.O. Box 11372, Marina del Rey, CA 90295, USA.

*Person to whom correspondence should be addressed. Email:
hkoopowi@uci.edu

ABSTRACT

Two species of *Narcissus*, *N. tortifolius* and *N. dubius* bear similarly sized, shaped and colored flowers. Both are thought to be derived from hybridization events involving *N. papyraceus* subsp. *panizzianus*. *Narcissus tortifolius* is rare, and *N. dubius* is common. We compared the fruit set, seed production, seed weight in one population of *N. tortifolius* with 5 disjunct populations of *N. dubius*, and found that the two species differed significantly in the percentage of flowers that set fruit and the percentage of ovules per ovary that developed into mature seed. There was no difference in seed weight. The rarer species may be pollinator limited with the result that reproductive costs in terms of numbers of flowers needed to produce equivalent numbers of seed are substantially higher.

The Iberian peninsular is a center of biodiversity for several geophytic plant taxa of which 194 monocotyledonous species are endemic. More than half of these fall into the various IUCN threatened categories (Moreno Saiz and Sainz Ollero, 1992) and about one quarter are considered to be rare. Understanding the underlying basis of rarity may help in formulating ways of conserving the diverse rare species and much attention has been focused on it (Gaston, 1994; Kunin and Gaston, 1997), particularly with respect to its importance for biodiversity conservation (Falk and Halsinger, 1991). The causes for rarity can be many and they vary with the organism under investigation.

The genus *Narcissus* L. is primarily Mediterranean in distribution with its largest center of diversity in the Iberian Peninsula. Estimations of the number of species in the genus vary but there are approximately 64 recog-

¹ This paper was peer-reviewed by two scientists before publication.

nized species (Blanchard 1990) with many distinct subspecies. Natural hybrids are frequent, even between widely different coexisting species. Few of these hybrids ever survive to form their own populations or develop into distinct and recognized species. Two such species of purported hybrid origin are *N. dubius* Gouan and *N. tortifolius* Fernández Casas. These two species are thought to have been derived by hybridization from *N. papyraceus* Ker-Gawler or *N. papyraceus* subsp. *panizzianus*. *Narcissus papyraceus* has $2n = 22$. *Narcissus dubius* is thought to be an allopolyploid $2n = 50$ containing one diploid set of chromosomes from *N. papyraceus* and a $4n$ set derived from *N. assoanus* Léon-Dufour [$n = 7$ (Fernandes, 1937, 1967)]. *Narcissus dubius* is a widely distributed species with many disjunct populations ranging from southeastern Spain to southern France. It is not known if these are derived from a single hybridization event or if there might be several independent origins of this hybrid. *Narcissus tortifolius* is only known from a few locations in southern Spain (Barra, 1999 and Sánchez Gómez et al., 2000). It is thought to be derived from *N. papyraceus* x *N. gaditanus* Boissier & Reuter (A. Fernandes, pers. comm. in Romero et al. 1983). Here, $2n = 36$, with one set of chromosomes derived from *N. papyraceus* and the other set from *N. gaditanus* ($2n = 14$). Blanchard (1990) cites Fernández Casas (no date) with the above observation, but there are two other initial reports (Fernández Casas, 1977, 1978) where $2n$ was initially reported as 22 and this number was later confirmed. The exact situation for *N. tortifolius* thus remains somewhat obscure. Romero et al. (1983) as quoted in Sánchez Gómez et al., (2000) reported $2n = 36$ for this species.

The flowers of these two species resemble each other and are of similar size. Both species have white blossoms and look like small flowered forms of *N. papyraceus*. Both *N. assoanus* and *N. gaditanus* have bright yellow flowers. Vegetatively, neither *N. dubius* nor *N. tortifolius* is really intermediate between their purported parents. Both species appear to have evolved specific adaptations that are unique in the genus. *Narcissus dubius* usually bears a single pair of prostrate, glaucous leaves that are flattened in cross section. *Narcissus assoanus* has several pairs of apple green, narrow and terete leaves, while *N. papyraceus* usually has several pairs of large erect glaucous leaves that are "D-shaped" in cross section. The leaves in *N. tortifolius* are peculiar within the genus. Each bulb produces several pairs of large erect leaves that spiral along their long axis. Leaves are oval in cross section and lack the channels and grooves seen in many other *Narcissus* species. Both *N. dubius* and *N. tortifolius* have leaves that appear to be adapted specifically for xeric environments. This

suggests that the purported hybridization events giving rise to these taxa must have occurred long enough ago to allow time for evolution to have changed the morphology of the plants.

Breeding systems in *Narcissus* are highly variable (Barrett, Jesson and Baker, 2000; Barrett, Lloyd and Arroyo, 1996). One species, *N. triandrus* L. (Barrett et al., 1997; Sage et al, 1999) is tristylous, while another, *N. albimarginatus* D. & U. Müller-Doblies (Müller-Doblies and Müller-Doblies, 1989) is distylous (Arroyo and Barrett, 2000). Some narcissus species such as *N. dubius* possess stylar length dimorphisms (Baker, Thompson and Barrett, 1999a and b; Dulberger, 1964) with long or short styled morphs within the same species. Here some populations may be of mixed length morphs while others populations are entirely long style morphs (Baker, Thompson and Barrett, 1999a and b). Other species, such as *N. pseudonarcissus*, are all long styled. In many *Narcissus*, self-incompatibility is said to be widespread (Barrett, Lloyd and Arroyo, 1996). Reports suggest that pollinator visitations for many *Narcissus* species are rare (Barrett, Lloyd and Arroyo, 1996, Fernandes, 1964), and for at least one species, *N. longispathus* Pugsley, fruit set is pollinator limited (Herrera, 1995). Our observations (Koopowitz, Aubrey and Donnison-Morgan, unpublished) on the fall flowering species, *N. cavanillesii* Barra & López and *N. serotinus* Parlato in Andalusia, Spain; and *N. elegans* (Haworth) Spach and *N. serotinus* in Morocco, suggest that fruit set is not always pollinator limited. In fact, we observed no flowers at those sites that failed to set fruit. It is not known how common pollinator limitation to fruit set is in other spring flowering species of *Narcissus*.

The current conservation status of *N. tortifolius* is listed as “vulnerable”, whereas that of *N. dubius* is “not threatened” (Moreno Saiz and Sainz Ollero, 1992). It would be interesting to know why *N. dubius* is common and *N. tortifolius* so rare. While there can be many reasons to account for rarity, here we hypothesize that differences in reproductive fitness may be contributing factors that help account for variation in distribution of the two species and we demonstrate that *N. dubius* is more efficient at seed production than *N. tortifolius*.

MATERIALS AND METHODS

We visited one population of *N. tortifolius* and five populations of *N. dubius* in March, 2001, (Table 1). All of the *N. dubius* populations we visited had long styled morphs with the stigma usually situated just beyond the two-ranked whorls of anthers. The situation in *N. tortifolius* is unknown, as the

Table 1. Site locations for the narcissus populations examined. Exact locality details are omitted for conservation reasons.

Species	Region	Locality	Notes	Altitude
<i>N. tortifolius</i>	Almería; Sierra Cabrera	N37.04; W02.04.	Among stunted bushes	400 M
<i>N. dubius</i>	Castellón; between Segorbe and Gátova	N39.49; W00.30.	North facing slope	450 M
	Castellón; Alto de Montmayor	N39.49; W00.30.	Open woodland	450 M
	Valencia; Alzira at Muntanyeta de San Salvador	N39.07; W00.37.	Surrounded by the town of Alzira, pine forest.	24 M
	Valencia; Barxeta	N39.00; W00.16	High altitude, grasses and forbs	700 M
	Alicante; Santa Eulalia		Very xeric	500 M

Table 2. Fruiting success in one population of *Narcissus tortifolius* and 5 populations of *N. dubius*.

Species	Number of umbels sampled	Total number of flowers	Total number of fruits	Percent fruiting success
<i>N. tortifolius</i>	55	319	173	54.23
<i>N. dubius</i>				
#1	75	167	167	100
#2	40	143	136	95.10
#3	164	605	547	90.41
#4	16	46	42	91.3
#5	127	219	215	98.17
TOTAL	422	1180	1107	93.81

Table 3. Ovule and seed production in *Narcissus tortifolius* and *N. dubius*.

Species	Total number of ovules	Average ovule number per capsule	Total number of seeds	Average number of seeds per capsule	Percentage yield ovules/seeds
<i>N. tortifolius</i> (n = 10)	536	53.6	526	52.6	60.83
<i>N. dubius</i> n = 17	828	48.7	687	40.4	82.97

entire population had finished flowering by the time that we assessed them. Both species are confined to north-facing slopes and occur in limestone areas. We were able to find and analyze a total of 426 inflorescences for *N. dubius* and 72 inflorescences for *N. tortifolius*.

***Narcissus tortifolius*.** The site for *N. tortifolius* was visited shortly after the flowering season and umbels had well developed fruit. Pedicels belonging to florets that did not set fruit were obvious in the umbels. It was possible to count the number of flowers produced and the numbers of seed set in each umbel examined. Two transects through the population yielded 72 umbels. A complete census of the entire population was not carried out, but we estimate it contained many hundreds of plants.

***Narcissus dubius*.** Inspection for this species occurred in the middle of its flowering season, and populations had flowers at all stages of development. The umbels that we sampled with developing fruit represented the earlier flowering plants in those populations. The populations ranged in size from less than one hundred to many hundreds of individuals. All of the umbels bearing fruit were examined in these populations. Mature capsules of *N. dubius* were found only at Monieta del San Salvatore in the town of Alzira. These were harvested and treated similarly to those of *N. tortifolius*.

For both species, mature capsules were harvested prior to dehiscence, and stored in separate paper envelopes until dry and dehiscent. The entire contents of each capsule were dislodged onto a piece of clean paper. It was easy to discern between fully formed seed and aborted/unfertilized ovules, and both were counted for each capsule. Capsule contents were weighed and average seed weight calculated.

RESULTS

We used several different measures to assess fitness. These included the number of florets on the umbel, the percentage of florets making fruits, the number and percentage of ovules producing seeds, mean seed weight, mean number of seeds per capsule, total seed production per umbel, and the number of florets needed to produce an equivalent number of seeds. Seeds were also sown and maintained under identical conditions and percentage of seed germination analyzed.

Floret production. The number of florets produced in an umbel was variable for each species (Table 2). The mean number of florets was 5.8 (range 2-11) in *N. tortifolius* and 2.7 (range 1-8) in *N. dubius*; however, there was variation in mean flower number per umbel among the 5 popula-

tions of *N. dubius*. In *N. dubius* we measured multiple spikes on some plants and found that even within a single clone there was variation in the number of florets produced. The largest clump was found at Monieta del San Salvatore, and it produced 8 inflorescences; 2 umbels bore 2 flowers each, 2 umbels had 3 flowers each, 1 umbel carried 4 flowers, while 2 each had 5 and there was a single inflorescence with 6 umbels. Other clones encountered at other sites had similar variations, although usually with fewer inflorescences.

Fruit production. We examined 72 inflorescences of *N. tortifolius* and found that 17 (23.61%) had been damaged and bore no fruit. Presumably, the goats that were herded in the study area were responsible for this damage. Of the remaining 55 inflorescences, 13 (23.63%) also bore no fruit. Thus for this population 41.67% of the total inflorescences were not productive. The 55 undamaged umbels bore 319 flowers, of which 173 (54.23%) successfully made fruits. Fruiting success in *N. dubius* (Table 2), was much higher, having an average fruit set ranging between 90.41 to 100% with a mean of 93.81% across all flowers. The difference between the two species was significant ($t = 21.8$, $p < 0.001$).

Seed production. Ten fruits of *N. tortifolius* were allowed to ripen and the number of mature seeds calculated as a percentage of the number of ovules produced (Table 3). The number of ovules in any one fruit varied from 38 to 58 (mean = 53; $n = 10$) while the number of mature seeds ranged from 19 to 52 (mean = 32.6). The average percentage of ovules forming seeds was 61%.

The number of ovules per ovary of *N. dubius* ranged from 38 - 60 (mean = 48.7; $n = 17$) and the mean number of seeds that matured was ranged from 25 to 52 (mean = 40.4; $n = 17$). The percentage of ovules producing seed was 83%. The differences in percentage yield between the two species were significant at the $P < 0.001$ level using a Monte Carlo contingency table.

Seed weight. Seed from eight capsules of *N. tortifolius* were weighed and the average weights per seed calculated. Mean seed weight ranged between 1.76 and 5 mg. The mean of the mean seed weight per seed capsule for an individual seed was 3.41 mg. Similarly the average individual seed weights for *N. dubius* were calculated from 12 seed capsules and ranged from 2.6 mg to 5.64mg. The average of the means was 3.49 mg. Differences in seed weight between the two species were not significant (ANOVA, $F [df_1, df_2] = 0.03$, $P = 0.86$).

DISCUSSION

Fitness is usually taken to be the measure of an individual's reproductive success. The question here is: do the members of *N. dubius* populations have greater fitness than the individuals of *N. tortifolius*, and if so, is this difference sufficient to account for the ubiquity of the former species and the rarity of the latter species? In terms of individual flowers, the fruit-set data show clearly that a *N. dubius* flower has a greater probability of being pollinated than a *N. tortifolius* flower. Although the number of ovules per ovary and seed weight do not differ significantly between the two species, *N. dubius* ovules have a greater probability of developing into seeds than do *N. tortifolius* ovules. But *N. tortifolius* plants tend to bear more flowers per umbel than inflorescences of *N. dubius*. However, the relative increases in fruit set for increases in flower number (Fig. 1) suggest that *N. dubius* gains additional fruit for flower number increase at approximately twice the rate of *N. tortifolius*, a highly significant difference (ANCOVA, $P < .0001$, $F \text{ ratio} = 43.8606$).

Considering single scapes, there are at least four limiting factors to reproductive success in these *Narcissus* taxa: 1) the number of flowers produced per umbel, 2) the number of flowers successfully pollinated per umbel, 3) the amount of pollen deposited on the stigma, and 4) the number of available ovules that develop into seeds.

The mean number of flowers borne by *N. dubius* for all five populations was 2.8 florets per umbel. This number of flowers is expected to contain 136

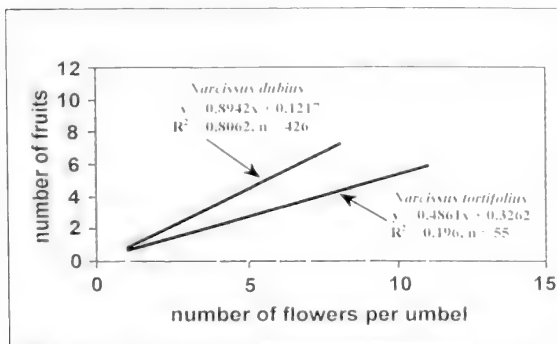


Fig. 1. Relationships between the number of flowers in an umbel and the numbers of fruits produced for both *N. dubius* and *N. tortifolius*. Only regression lines are shown here. Both regressions are significant, that of *N. dubius* at $P < 0.001$ and *N. tortifolius* at $P < 0.01$ level. Using an ANCOVA the difference between the two regression lines is also significant at the $P < 0.0001$ ($F [df_1, df_2] = 43.8606$).

ovules, of which 113 will develop into mature seeds. However, only 94% of the flowers formed fruits. The actual average seed production per umbel was therefore 106. The mean numbers of flowers per umbel varied with the population counted. It ranged from 1.7 flowers in the Ste. Eulalia population to 3.9 florets per inflorescence in

the Monieta del San Salvadore population. This latter was nearly a third more than the combined average from all five populations. Although there was variation in the reproductive efficiency among populations of *N. dubius*, it is useful to use the lower average figures for comparison with *N. tortifolius*.

N. tortifolius produced an average of 5.8 flowers per umbel, and the ovaries contained an average of 310 ovules in each inflorescence. Seed production would have been 189 seeds had every flower been pollinated, but the average percentage of the flowers that make fruit is only about half (54%). Thus the actual average seed production per umbel is expected to be only 102.5.

Although it appears that on the average each *N. dubius* plant that flowers produces an equivalent number of seeds to *N. tortifolius*, the costs are quite different. *N. tortifolius* must produce twice the number of flowers per inflorescence and 2.3 times the number of ovules to achieve the same number of seeds as *N. dubius*. Some *N. dubius* populations, such as Monieta del San Salvadore (#3), are even more efficient.

Narcissus tortifolius flowers during the winter and *N. dubius* is spring flowering. The possibility exists that the differential seed set involves some form of pollinator limitation because of seasonal restraints. The data suggest that pollinator limitation probably plays a minor role for *N. dubius*, but it may be important for the winter flowering *N. tortifolius*.

Orians (1997) pointed out some possible evolutionary consequences of small, rare populations. Among these is natural selection favoring self-compatibility. Thus one might expect that the varied breeding systems in *Narcissus* should reflect the size and isolation parameters of their component populations. *N. dubius* is highly self-compatible (Baker, Thompson and Barrett, 2000a and b) but the situation in *N. tortifolius* does not appear to have been investigated. *N. papyraceus*, one of the purported parental species, has some populations that are monostylus and others that are distylus (Barrett, Lloyd and Arroyo, 1996). The monostylus populations all had long-styled flowers. They also reported that *N. gaditanus* was distylus, although one population had a very small proportion (6%) of short styled flowers. On the other hand, both of the populations of *N. assoanus*, the other possible parent of *N. dubius*, had 28-38% short styled individuals. All of the *N. dubius* populations we observed in Southern Spain only had long styled flowers. In contrast, Baker et al. (2000 a and b) reported some distylus *N. dubius* populations. The situation in the *N. dubius* populations that we studied suggests a limited number of ancestors for these populations.

The absence of short styled morphs could therefore be fortuitous and unrelated to reproductive fitness.

The *N. tortifolius* population we examined exists within the confines of a nature preserve. The reserve offers little protection to this rare species. We observed goats grazing within a few hundred meters of the plants, and this could account for the damaged inflorescences that we observed. Nearly a quarter of the umbels in the population had been bitten off at the level of the pedicels or through the peduncle itself. All of the flowers were cut off at the same level within each umbel, consistent with goat browsing. For a species that is classed as vulnerable, these levels of damage may be unsustainable, but because of the long-lived nature of this species and the long generation times, the full effects of browsing may not be obvious for an equally long period of time.

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**FRITILLARIA CRASSIFOLIA SSP. KURDICA (LILIACEAE):
A BEAUTIFUL BULBOUS PLANT IN IRAN**

Gholamreza Bakhshu Khaniki

Department of Biology, Payame Noor University
P. O. Box 19395-4697, Tehran, Iran

ABSTRACT

A key, description, nomenclatural synonymy, citation of specimens examined, and morphological, taxonomic ecological and karyological details are given for *Fritillaria* ssp. *kurdica* (Liliaceae) in Iran. The linear nectaries are about 8–10 by 1.5–2 mm, with a dark purplish, swollen ridge along the inside center of the tepals, and often more blackish at the base. Sparse warts on the tepal surface surround them. The species grows mainly in screes, mountain steppe, grassy and rock ledges, dry stony slopes and the border of fields, in some localities close to snow patches. The somatic chromosome number is $2n = 24$.

INTRODUCTION

Although comparatively little has been written about *Fritillaria* over the course of history, the genus has been known for many centuries. The old herbals show woodcuts of a number of species, albeit in many cases not easily reconciled with the attached names. According to Beck (1953), the earliest of these are probably Pena and l'Obel (1570), and Gerarde (1636). Linnaeus (1753), who established this genus, included four species, *F. imperialis*, *F. persica*, *F. meleagris* and *F. pyrenaica* in his Species Plantarum. The genus now includes approximately 125 species growing in temperate regions of the northern hemisphere (Bakhshi Khaniki, 1998), except eastern North America. All Iranian species of *Fritillaria* belong to the subgenera *Fritillaria*, *Petilium*, and *Theresia*. Of the four main groups within *Fritillaria* subgen. *Fritillaria* in Western Asia and Europe, three occur in Iran. These are the *F. crassifolia* group, the *F. kotschyana* group and the *F. caucasica* group. *F. crassifolia* ssp. *kurdica*, the subject of the present study, belongs to the *F. crassifolia* group, which is morphologically distinguished by having broadly campanulate flowers (narrowly campanulate in *F. poluninii*) that generally nod at maturity, and linear nectaries that are half or more than half as long as the perianth segments and situated 3–5 mm above their base. The aim of the present investigation is to report the latest data about taxonomy, ecology, morphology and karyology of *F. crassifolia* ssp. *kurdica* in Iran.

TAXONOMY AND DESCRIPTION

Key to the subgenera of *Fritillaria* represented in Iran:

1. Bulb of several erect imbricate fleshy scales; flowers in an umbel overtopped by a group of many bract leaves *Fritillaria* subgen. *Petilium*
1. Bulb of a single massive fleshy ovoid scale or usually of 2 (sometimes 3–4) fleshy or farinaceous subglobose scales; flowers in a raceme or solitary 2
 2. Bulb of a single fleshy ovoid scale; flowers arranged in a 6–20 (–38) flowered raceme with short or no bracts; filaments glabrous; style glabrous, entire *Fritillaria* subgen. *Theresia*
 2. Bulb of 2, sometimes 3–4, fleshy or farinaceous subglobose scales; flowers solitary, sometimes 2–3, rarely more per stem, with \pm leaf-like bracts; filaments often papillose; style papillose or glabrous, entire or trifid.... *Fritillaria* subgenus *Fritillaria*

Key to the Iranian species groups of subgenus *Fritillaria*:

1. Flowers broadly campanulate; nectaries c. 5–7 mm above base of perianth segments 2
1. Flowers narrowly campanulate, rarely rounded (\pm urceolate); nectaries at or 0.2–2 mm above the base of perianth segments *Fritillaria caucasica* group
 2. Nectaries linear, more than half as long as the limb of the perianth segments *Fritillaria crassifolia* group
 2. Nectaries ovate to lanceolate, less than half as long as the limb of the perianth segments *Fritillaria kotschyana* group

Key to the Iranian species of the *F. crassifolia* group:

1. Flowers pale purple to greyish with dark purple or greenish veins, hardly tessellated, held very open at maturity; without fascia; nectaries without raised ridge, usually 4–5 mm long *F. poluninii*
1. Flowers usually stippled and tessellated inside and outside on a yellowish ground, often with green fascia; nectaries with raised ridge, usually 9–12 mm long *F. crassifolia* ssp. *kurdica*

F. crassifolia* ssp. *kurdica (Boiss. and Noë) Rix. (Fig. 1). Rix, Kew Bull. 29 (4): 638 (1974).

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[*F. racemosa*. sensu Grossheim, Fl. Kavkasa 1: 221 (1928), non Ker-Gawler.]

lc.: Rix, Iran. J. Bot., Fig. 4 (1977).—Turrill and Sealy, Hooker's Icones Plantarum 39 (1 and 2), t. 3824 (1980).—Rix and Phillips, The Bulb Book, p. 82, Figs. a and c (1981).—Mathew and Baytop, The Bulbous Plants of Turkey, Fig. 87 (1984).—Rechinger, Flora Iranica 165, t. 174, Fig. 3 (1990).

Bulb ovoid to subglobose, 1.5–2 x 1–2 cm, of two fleshy scales; bulbils present, without stolons. Stem 6–24 cm, smooth. Leaves 4–7, all alternate (the lowest sometimes subopposite), glaucous; the lowest 3–7 x 0.5–2 cm, lanceolate, apex obtuse; the upper narrower, linear. Flowers 1–2(–4), broadly campanulate, greenish to yellowish, \pm heavily tessellated with brown inside and outside, often with green fascia; perianth segments 23–24 x 8–12 mm, obovate to oblanceolate, obtuse, with hairy apices, the inner ones wider. Nectaries 8–10 x 1.5–2 mm, linear, with a dark purplish, swollen ridge along the inside center, often more blackish at the base, placed 3–5 mm above base of the perianth segments, surrounded by sparse warts on tepal surface. Filaments 6–10 mm long, yellowish-green, papillose. Anthers 2.5–5 mm long after dehiscence, yellow; pollen sculpture macroreticulate, exine surface smooth. Style 5–9 mm long, trifold for 1/5 to 1/4 of its length, branches 1–2 mm long, glabrous. Ovary 5–6 mm long, stoutly cylindrical. Capsule 4–4.5 cm long, obovoid, narrowly tapering at base, truncate at apex, not winged. Seeds 5.5–6 mm long, ovate in outline. Chromosome number: $2n = 24$ (Bakhshi Khaniki 1998)

Specimens examined:

Iran: *E. Azarbaijan*: Tabriz to Ahar, pass c. 20 km south-west of Ahar, among stones, 1700 m, 25.4.1976, Wendelbo and Assadi 19430 (GB, TARI); 62 km after Mianeh on road to Tabriz, stony slopes, 1700 m, 21.4.1976, Wendelbo and Assadi 19194 (GB, TARI); Marand, Khoy to Tabriz road, on stony banks near river, sparse grazing, 2031 m, 11.5.1963, Mathew in BSBE 1509 (K), 2000 m, 12.5.1994, Bakhshi Khaniki 72 (GB); Kuh-e Sahand, north side above Liqvan, stony slopes among grass and lucern, 3125 m, 31.5.1962

(type locality of *F. grossheimiana*), FURSE 2333 (K), 2031 m, 25.5.1960, Syngé and Furse 247 (K), 2850 m, 10.5.1994, Bakhshi Khaniki 71 (GB); south-west of Ahar, 1800 m, 30.5.1971, Rechinger 40614 (G, W); 44 km from Shebli towards Mianeh, 1850 m, 6.5.1971, Rechinger 39321 (W).—*Ardebil*: southern foothills of Kuh-e Sabalan, 20 km west of Ardebil, 2500 m, 6.6.1962, Furse 2423 (W), 2600–2800 m, 13.5.1994, Bakhshi Khaniki 74 (GB).—*W. Azarbaijan*: Urmiah, Anbee valley, Sero road, 1400–1450 m, 14.8.1976, Kohafkane and Amini 7292 (K, TUH); Urmiah, Sir Kuh, c. 2000 m, rocky ground in deep loam, 8.5.1963, Mathew in BSBE 1434 (K); in mountain slopes of Salmas area, Szovits (G); north-east foothills of Aghvan Dag, 64 km from Rezaiyeh, rocky slopes, c. 3200 m, 24.5.1962, Furse 2253 (W), 1900–2100 m, 13.5.1994, Bakhshi Khaniki 73 (GB); road from Urmiah to Salmas, 70 km to Salmas, Ghushchi pass, Avech Mishaeh valley, 2110 m, 7.5.1994, Bakhshi Khaniki 62 (GB).—*Tehran*: road from Karaj to Chalus, Chalus pass, 2200 m, 20.5.1994, Bakhshi Khaniki 103 (GB); Lavasanat, northern slopes of Gachsar, 2500 m, 19.5.1994, Bakhshi Khaniki 96 (GB). *Turkey*: *Hakkari*: Sat Dag, north-west of Sat Gölu, 2900–3000 m, by melting snow, 28.6.1966, Davis 45682 (GB); Sat mountains, rocky pasture, 2800 m, 5.4.1965, Fedden and McColl 17 (K); Mor Dag, stony patches, 3250 m, by melting snow, 29.6.1967, Cheese et al. 2978 (K).—*Van*: Gevas, Artos Dag, with *Tulipa*, 3000 m, 16.7.1954, Davis 22780 (GB); *ibid.*, rocky north slope, c. 3000 m, 15.7.1954, Davis 22809 (K); Pelli Dag, between Van and Tetran, 6.7.1968, Rix 794 (K); *ibid.*, c. 3000 m, 1.7.1968, Rix 743 (K); pass 30 km west of Gevas, lake Van, on shale slopes near melting snow, 2000 m, Mathew and Tomlinson 4217 (K); Gevas, 1900–2000 m, 22.5.1972, Hower 2139 (K); Karedagh, 12.6.1944, Bornmüller 57 (JE); Van, Warak (=Erek) Dag, 1.6.1899, Kronenburgh 61 (JE, G, type of *F. wanensis*); Baskale, 2800 m, 26.5.1966, Eiselt (W).—*Bitlis*: Tatvan, on the south of the town, 10.5.1975, Rix 1975 (K). *Iraq*: Haji Omran, stony slopes, c. 2800 m, 14.4.1968, Polunin 5063 (K).

NECTARY MORPHOLOGY

Fritallaria crassifolia ssp. *kurdica* (Boiss. and Noë) Rix differs from ssp. *crassifolia* by its higher number of leaves, which are also proportionally narrower, and in its flowers that have more clearly defined fascia. It is usually a dwarf plant, very variable in flower color. The flowers are greenish to yellowish, \pm heavily tessellated with brown inside and outside, often with green fascia. The perianth segments are 23–34 x 8–12 mm, obovate to oblanceolate and obtuse. The apex of the tepals is papillose (Fig. 2C). The linear nectaries are about 8–10 x 1.5–2



Fig. 1. *Fritillaria crassifolia* ssp. *kurdica*. A. Sample collected from Kuh-e Tiz Tiz, Kordestan province. B. Habitat.

mm, with a dark purplish, swollen ridge along the inside center of the tepals, and often more blackish at the base and is surrounded by sparse warts on the tepal surface (Fig. 2A-B, D-F). They continue and taper toward the tepal apex by a narrow zone divided longitudinally by a channel. The basal part of the nectary is apparently more active in nectar sugar secretion because it is usually filled with a watery fluid which seems to trickle along the median furrow, i.e. downwards in the hanging flowers. Further detail on nectary morphology in *Fritillaria* and *Rhinopetalum* is given in Bakhshi Khaniki and Persson (1997).

ECOLOGY

Fritillaria crassifolia ssp. *kurdica* flowers in April to July and mainly grows in screes, mountain steppes, grassy and rock ledges, dry stony slopes and border of fields from 1400 to 3200 m. In some localities flowering plants are found close to snow patches. It is also known from Turkey, Iraq and Armenia. The *F. crassifolia* group consists of a complex of species and subspecies close to *F. crassifolia* centered on eastern Anatolia and the northern Zagros mountains. Two morphologically distinct species in the group are *F. reuteri*, found in the central Zagros Mountains, and *F. straussii* in the northern Zagros Mountains, extending into Hakkari. The most widespread member of the complex is *F. crassifolia* ssp. *crassifolia* which occurs in Turkey from Erzerum in the north-east to Muglail in the southwest. It occurs most commonly on mobile scree. Subspecies *kurdica* is frequent on alpine steppe in the mountains south of Lake Van, in northeast Iraq and throughout Azarbaijan. Subspecies *hakkarensis* occurs in Hakkari and northern Iraq. The former subspecies *poluninii*, recently raised to specific level (*F. poluninii* (Bakhshi Khaniki and Persson, 1997), occurs in Hakkari, northern Iraq, and northwest Iran.

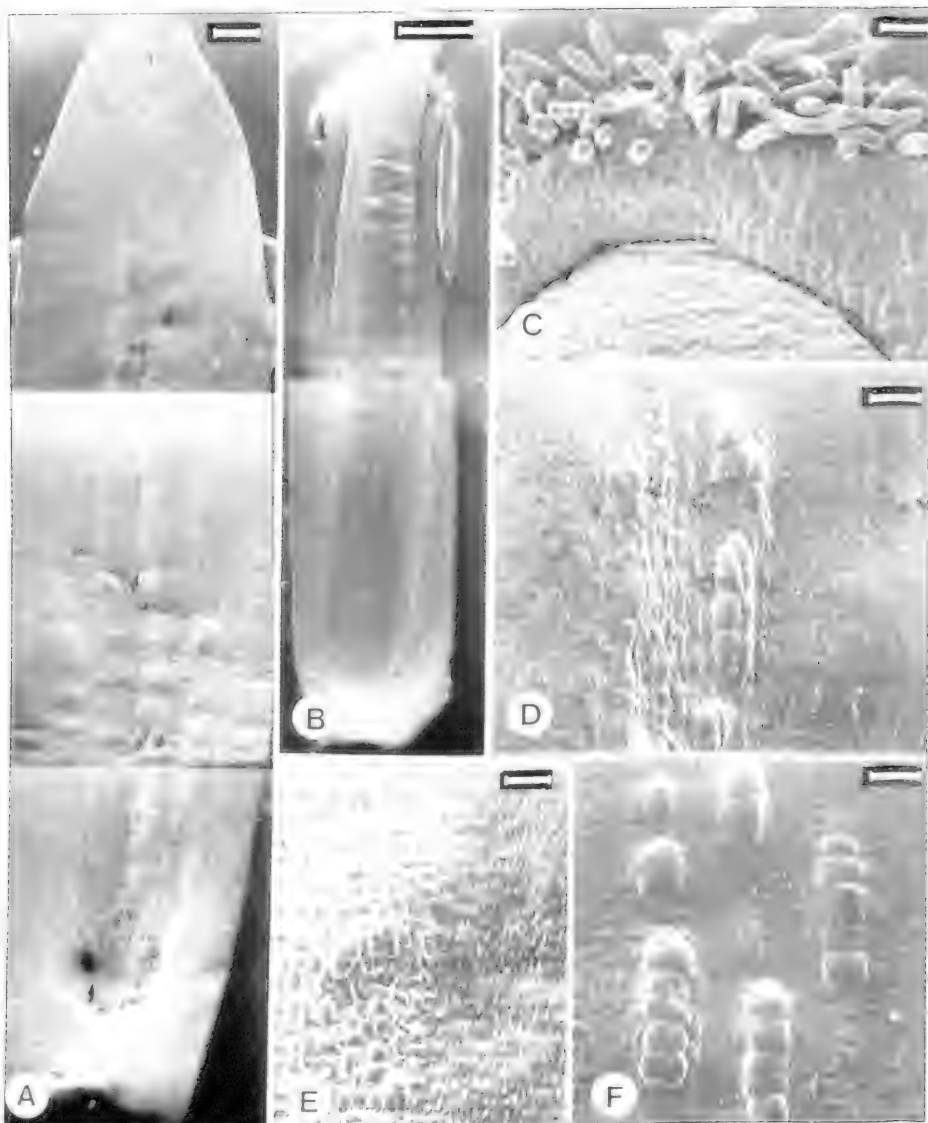


Fig. 2. Scanning electron micrographs of *Fritillaria crassifolia* ssp. *kurdica*. A. Nectary on outer tepal (the tepal was cut in 2 pieces before drying). B. Nectary on inner tepal. C. Papillose apex of inner tepal. D. Ridges and warts on nectary border of outer tepal (nectary to the right). E. Cells from nectary border on inner tepal (nectary to the right). F. Groups of warts and short ridge-like processes on tepal surface. Scale bars: A, 1mm; B, 2mm; C-F, 100 μ m.

Subspecies *kurdica* is very variable in overall size and in flower color, and many names have been given to minor variants. Based on my field studies, the samples collected from eastern Azarbaijan have more distinct fascia and darker purplish brown perianth segments, while those from the Elborz Mountain in the Tehran region have less defined fascia and more greenish flowers, but the two forms hardly merit formal recognition. Many forms have been described as distinct species, e.g., *F. karadaghensis* Turrill, *F. foliosa* Bornm. from Mt. Karedagh in Tabriz (eastern Azarbaijan), and *F. grossheimiana* Los.-Losinsk. from Mt. Sahand, also in Tabriz. *F. wanensis* was recorded from subalpine regions near Lake Van in northeastern Turkey, where the type material of *F. kurdica* was collected by Noë. None of these forms seem worthy of taxonomic recognition even at the varietal rank. Subspecies *kurdica* differs from ssp. *crassifolia* in having proportionally narrower leaves and more clearly defined fascia. It differs from ssp. *hakkarensis* particularly by its glaucous. *F. poluninii*, which originally was described as a subspecies of *F. crassifolia*, differs from subspecies *kurdica* by having unraised (smooth) and short nectaries, narrow leaves and perianth segments, and smaller, paler and narrowly campanulate flowers. Furthermore, subspecies *kurdica* is distinguished from species belonging to the *F. kotschyana* group by having linear as opposed to ovate nectaries. It differs from *F. straussii* in having all alternate leaves and papillose styles, and from *F. reuteri* by the color and tessellation of the perianth segments.

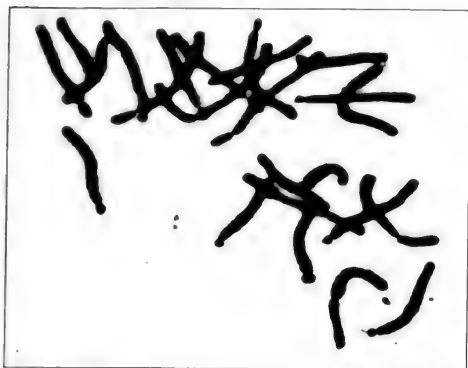


Fig. 3. *Fritillaria crassifolia* ssp. *kurdica*, mitotic metaphase, $2n = 24$.

KARYOLOGY

The somatic chromosome number is $2n = 24$ and the haploid karyotype consists of two metacentric, one submetacentric, five subtelocentric and four telocentric chromosome pairs (Fig. 3). More details about karyotype and C-banding is given in Bakhshi Khaniki (1998).

ACKNOWLEDGEMENTS

I wish to thank Dr. Karin Persson and Prof. Lennart Andersson (Department of Systematic Botany, Gothenburg University, Sweden) for reading the manuscript, and providing constructive criticism and helpful suggestions.

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**FRITILLARIA ZAGRICA (LILIACEAE):
AN ENDEMIC SPECIES OF FRITILLARY IN IRAN**

Gholamreza Bakhshi Khaniki

Department of Biology, Payame Noor University

P.O.Box 19395-4697, Tehran, Iran

ABSTRACT

Fritillaria zagrica is a species endemic to Iran distributed throughout the Zagros Mountain chain in Iran. It is characterized by distinctly glaucous leaves and dark purplish-brown flowers with a yellow apex. The nectaries are lanceolate, only slightly sunken, 3.5–5 by 1–1.5 mm and purplish-green. A few warts and similar processes are scattered on the tepal surface. The flowering season is March to May. It grows in mountain steppes, often by late snow patches, in deep, moist, soil among rocks and large stones, screes and rock ledges at 1650 to 3000 m elevation. The basic karyotype in this species is $n = 12$, consisting of two metacentric, five subtelocentric and five telocentric chromosome pairs.

INTRODUCTION

The genus *Fritillaria* (Liliaceae) in Iran is relatively poor in species (ca. 15) compared with Turkey (ca. 31). According to Rix (1977, 1984), the *F. caucasica* group presents many taxonomic difficulties in Turkey due to frequent interspecific hybridization. In Iran, however, differences between species are more clear-cut, with fewer indications of introgression. Seven previously described species (Rechinger, 1990, Bakhshi Khaniki 1997a, 1997b) are found in Iran that belong to this complex: *F. caucasica* Adams, *F. zagrica* Stapf, *F. assyriaca* Baker, *F. uva-vulpis* Rix, *F. chlorantha* Hausskn. and Bornm, *F. atrolineata* Bakhshi Khaniki, and *F. chlororhabdota* Bakhshi Khaniki. The species of the *F. caucasica* group have comparatively small and narrowly campanulate flowers, with the nectaries usually placed at the base or 0.5–1 (–2) mm above the base of the perianth segments.

The aim of the present investigation is a morphological, ecological, taxonomic and karyological treatment of *Fritillaria zagrica* in Iran, using as much data as possible with the aid of light microscopy (LM), scanning electron microscopy (SEM), and chromosome studies.

TAXONOMY AND DESCRIPTION

F. zagrica Stapf. (Fig. 1). Stapf, Verh. Zool. Bot. Ges. Wien 38: 551 (1888).

Type: Iran, "von Elwand, von Sultanabad und von Kuh-i Barf bei Schiraz", Stapf (iso. W!). Ic.: Furse, The Lily Year Book 1964: Fig. 41 (1963).—Wendelbo, Tulips and Irises of Iran, Fig. 27 (1977).—Rix and Phillips, The Bulb Book, p. 78, Fig. b (1981).—Rechinger, Flora Iranica 165, t. 175, Fig. 1 (1990).

Bulb narrowly ovoid to subglobose, up to 2 cm in diameter, consisting of 2 fleshy scales; bulbils few, without stolons. Stem 5–12(–20) cm, often smooth, sometimes papillose at base. Leaves 4–12, usually 5–6, glaucous, generally alternate; the lowest sometimes subopposite, 3–9.5 x 0.5–1.5 cm, lanceolate, with a wavy edge, acute, the upper linear, acute. Flowers 1–2(–3), narrowly campanulate; perianth segments 12–18 x 4–7(–9) mm, dark purplish-brown with a yellow apex and a waxy bloom inside; the outer elliptic-lanceolate, acute; the inner usually oblanceolate, wider, obtuse. Nectaries 3.5–5 x 1–1.5 mm, lanceolate, only slightly sunken, green-purplish, placed 1 mm above the base of tepals. Filaments 7–9 mm long, purplish, slender, densely papillose. Anthers 3–4.5 mm long, purplish; pollen sculpture macroreticulate, exine surface rough due to small granulae. Style 7–9 mm,



Fig. 1. *Fritillaria zagrica*. A. Plant in cultivation (originally collected from Golestan-kuh, Khonar, Isphahan). B. Plant in fruit (Elwand Mountain, Hamadan). C. Habitat.

slender, entire, papillose. Ovary 4–5 mm long, cylindrical. Capsule 3–4 (–5) mm long, obovoid, not winged. Seeds 8 x 6.5 mm, ovate in outline.

Chromosome number: $2n = 24$ (Bakhshi Khaniki 1998).

Specimens examined:

Iran: *Lorestan:* 27 km north-east of Azna, near Mahmudabad, 1800 m, 17.5.1994, Bakhshi Khaniki 86 (GB).—*Esfahan:* Khunsar, Golestan kuh, 2600–2800 m, 2.5.1975, Wendelbo and Assadi 16386 (GB, W, TARI), 2656–2813 m, 3.5.1975, Ingham 146 (K), 2300–2600 m, 2.5.1993, Bakhshi Khaniki 15 (GB), 15.5.1994, Bakhshi Khaniki 89 (GB); Kuh-e Darabshah above Damaneh, in deep moist earth among rocks and large stones, close to snow patches, north facing, 2656 m, 15.4.1962, Furse 1438, 1743 (K, W, TUH); Golpaigan, Kuh-e Darrahbid, 2750 m, 18.5.1993, Bakhshi Khaniki 29 (GB).—*Arak:* Arak, north-east to east slopes of Kuh-e Barfkhaneh, 2300–2800 m, 4.5.1975, Wendelbo and Assadi 16474 (GB, TARI, TUH); Kuh-e Moudar, 1989, Haussknecht (JE); Salian, Strauss (JE); Arak (Sultanabad), 30.3.1982, 20.4.1895, Strauss 130 (JE); Arak, mountain Rasevend, May 1896, Strauss (JE); Sultanabad village, 1900 m, 23.3.1993, Bakhshi Khaniki 33 (GB); south of Arak, south-east of Azna, in rocky mountain slopes below limestones, 2812 m, 18.4.1962, Furse 1497 (K); 42 km from Arak to Esfahan, in steep slope above the road, 2160 m, 1.4.1969, Hewer 908 (K); Arak (Sultanabad), 12.5.1892, Bornmüller (G); Arak to Golpaigan, 40 km east of Arak, in shaly slopes, 2031 m, 23.4.1962, Furse 1572 (W); Arak to Borujerd, Kuh-e Sefidkhani, in screes and rock ledges, 12.6.1993, Bakhshi Khaniki 38 (GB), 15.5.1994, Bakhshi Khaniki 78 (GB); Sultanabad Stapf (type material, iso. W); Soltanabad village, Kuh-e Barfi and Girdu hills near Arak, in sandy soil with grasses, 1900 m, 17.5.1994, Bakhshi Khaniki 80 (GB).—*Qum:* Tefresh, 1899, Strauss (JE).—*Fars:* 60 km south of Abadeh, Kuh-e Bul, near Aghlid, 2850 m, 25.5.1975, Foroughi 17327 (GB, E).—*Hamadan:* road from Hamadan to Asadabad, 28 km west of Hamadan, Asadabad pass, 2300 m, 4.5.1994, Bakhshi Khaniki 69 (GB); Hamadan, Elwand kuh, near Ganjnameh, in stony sandy and granite slopes, 2400 m, 10.5.1975, Wendelbo and Assadi 16827 (GB, TARI), above Ganjnameh, 2500 m, 30.4.1994, Bakhshi Khaniki 60 (GB), Kuh-e Elwand, May 1897, Strauss (JE), Kuh-e Elwand, Stapf (type material, iso. W), Ekbatan, 2400 m, 5.5.1993, Bakhshi Khaniki 20 (GB); Qazvin to Hamadan, 32 km from Hamadan, in rocky hill with light loam, 1719 m, 20.3.1962, Furse 1108 (W); Hamadan to Sanandaj, east of

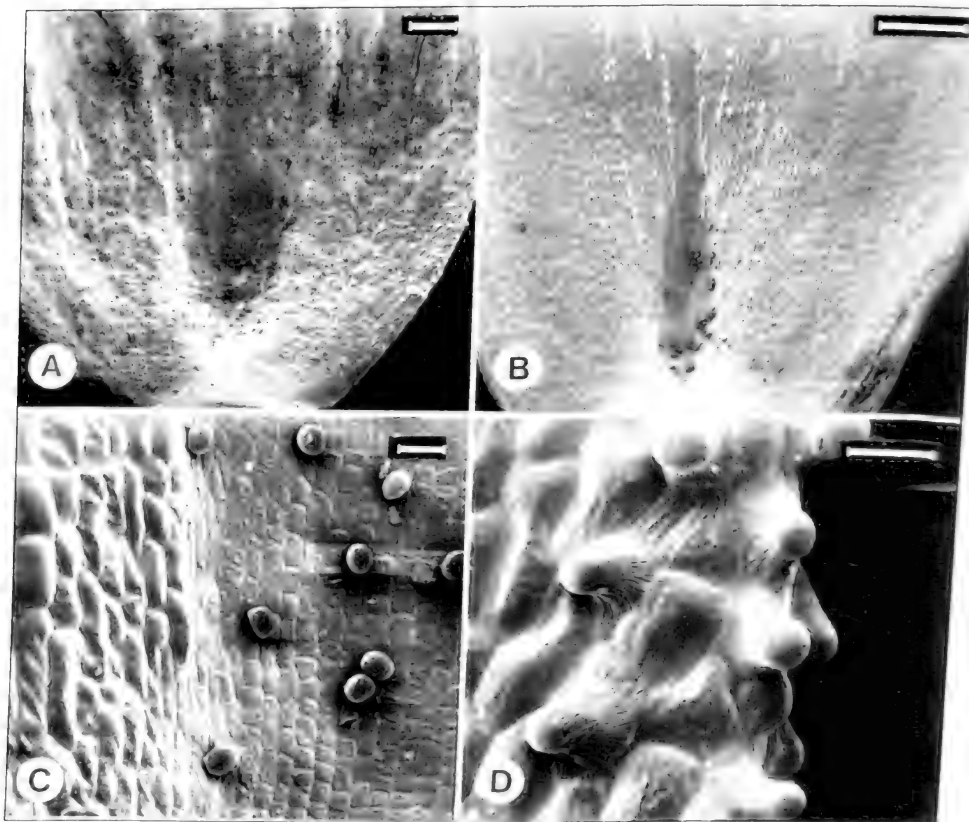


Fig. 2. Scanning electron micrographs of *Fritillaria zagrica*. A. Nectary on outer tepal. B. Nectary on inner tepal. C. Cells from nectary border on outer tepal (nectary with adherent pollen grains to the right). D. Papillae on tepal margin. Scales: A-B, 500 μ m; C-D, 50 μ m.



Fig. 3. *Fritillaria zagrica*, mitotic metaphase, $2n = 24$.

Sanandaj, sloping fallow field, 1875 m, 16.5.1962, Furse 2049 (W), 1650–1800 m, 5.5.1993, Bakhshi Khaniki 21 (GB); Hamadan, Aq Bulaq, c. 100 km north of Hamadan, 15.4.–1.7.1960, Rioux and Golvan 13 (W, G); Aghbolagh, 60 km from Bijar, 24.4–10.5.1956, Schmid (G).—*E. Azarbaijan*: Tabriz to Ahar, first pass, northern sides, 1650 m, 25.4.1976, Wendelbo and Assadi 19286 (GB, TARI); Band, near Urmiah (Rezaiyah), 1563 m, 14.5.1929, Cowan and Darlington 2089 (K).

NECTARY MORPHOLOGY

Within the *Fritillaria caucasica* group, species have comparatively small and narrowly campanulate flowers, and the nectaries are usually situated at the base or 0.5 to 1 (–2) mm above the base of the perianth segments (Bakhshi Khaniki and Persson, 1997).

In *F. zagrica*, the flowers are dark purplish-brown with a yellow apex. The outer tepals are 12–18 by 4–7 mm, elliptic-lanceolate and acute. The nectaries are lanceolate, only slightly sunken, 3.5–5 by 1–1.5 mm and purplish-green. A few warts and similar processes are scattered on the tepal surface (Fig. 2A-B). The tepal margins are papillose (Fig. 2C-D).

ECOLOGY

Flowering time: March–May.

Ecology and distribution: Mountain steppe, often by late snow patches, deep moist soil among rocks and large stones, screes and rock ledges, 1650–3000 m. Endemic to Iran.

Fritillaria zagrica is distributed all along the Zagros mountain chain in Iran, and is characterized by the rather distinctly glaucous leaves and dark purplish-brown flowers with a yellow apex.

KARYOLOGY

The basic karyotype in this species is $n = 12$, consisting of two metacentric, five subtelocentric and five telocentric chromosome pairs (Fig. 3). More details about karyotype and Giemsa C-banding pattern is given in Bakhshi Khaniki (1998).

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I wish to thank Dr. Karin Persson and Prof. Lennart Andersson (Department of Systematic Botany, Gothenburg University, Sweden) for reading of the manuscript, constructive criticism and helpful suggestions.

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NOMENCLATURE CHANGE OF A *CRINUM* SPECIES (AMARYLLIDACEAE FROM MADAGASCAR)

David J. Lehmiller, M.D.

550 IH-10 South, Suite 201, Beaumont, Texas 77707 U.S.A.

Perrier (1939) confused the identity of *Crinum firmifolium* Baker (1883) in his monograph of Malagasy *Crinum* (Lehmiller, 1992). In his treatment of *C. firmifolium*, Perrier devised a scheme wherein he subdivided this "species" into three varieties: var. *hygrophilum*, var. *geophilum*, and var. *xerophilum*. He cited strong affinity between *C. asiaticum* L. (1753) and *C. firmifolium*, and he postulated that after *C. asiaticum* had been introduced into Madagascar, climatic conditions in the various regions of Madagascar had transformed *C. asiaticum* into the three varieties of *C. firmifolium*. Perrier incorporated a number of unrelated species into this scheme, encompassing a diversity of umbel configurations, leaf morphologies, and bulb shapes which was contrary to all other taxonomic concepts of this genus. Alas, the scheme did not meet legitimacy, because Perrier equated other species with *C. firmifolium* Baker which had publication-date priority over *C. firmifolium*, a violation of Article 57 of the International Code of Botanical Nomenclature (1988). For example: 1) *C. firmifolium* var. *hygrophilum* was *C. asiaticum* L. (Verdoorn, 1983; Lehmiller, 1992), an alien species from Asia which had naturalized to Madagascar and to the nearby Mascarene Islands (Baker, 1877); 2) Perrier (1939, 1950) dismissed *C. hildebrandtii* Vatke (1876) as representing *C. firmifolium* Baker which merely had been transported from Madagascar to the Comoros Islands, and he never bothered to examine the type specimen or to acknowledge Malagasy specimens identified as *C. hildebrandtii* residing in the herbarium at Kew within the same folder as the type specimens for *C. firmifolium* Baker and *C. ligulatum* Baker; and 3) *C. firmifolium* var. *xerophilum* encompassed *C. voyronii* Jumelle (1924-25), the latter a synonym of *C. mauritianum* Loddige (1822). Furthermore, Perrier did not validly publish his scheme, omitting the required Latin descriptions (Article 36), and he did not designate holotype specimens for var. *xerophilum* and var. *hygrophilum*.

D. Hardy called my attention to a flowering bulb that he had collected near Morombe in Southwest Madagascar in 1972. He had discovered two small clumps of bulbs growing in sand in dry bush. Hardy thought that it was possibly an undescribed species, and he planned a collaborative publi-

cation of the new taxon with I. Verdoorn in *Flowering Plants of Africa*. When the bulb subsequently bloomed at Pretoria in 1983, it was illustrated for publication and a second herbarium specimen was arduously prepared, but the project to classify it as a new taxon never came to fruition. Hardy presented me with a large offset from his bulb in 1989 and requested that I investigate whether or not it was an undescribed species. The offset bloomed on three occasions in my greenhouse during the subsequent five years. During this interval, Hardy reported that he had located similar bulbs north of Tulear in Southwest Madagascar, one of which he collected on the road to Ifaty in dune sand and transplanted into the gardens at Parc de Tsimbazaza in Antananarivo (Fig. 1.).

During field trips with Hardy to Madagascar in November 1995 and November 1996, we visited Tulear to search for the bulbs, but as there had been no rainfall in the region for many months, we were unable to locate any. (The locality is arid, and the summer rains are unpredictable; often-times, significant summer rainfall only occurs during passage of a sporadic tropical storm or typhoon.) We returned in January 1998, and again there had been no summer rainfall. However, we did make a fortuitous discovery of a small clump of the subject bulbs on the road to Ifaty, 10 km north of Tulear. The semi-dormant bulbs were growing in dune sand on a hill overlooking the ocean, less than 200m from the shoreline. They were burrowed deep into the sand and had developed long underground necks (Fig. 2.).

The desert *C. firmifolium* var. *xerophilum* described by Perrier (but omitting his reference and discussion regarding *C. voyroni*) is the species that Hardy collected. It has unique characters among the indigenous Malagasy species within subgenus *Crinum* and warrants separate recognition. Foremost, it bears pedicellate flowers; all other members in subgenus *Crinum* possessing sessile or subsessile flowers. Secondly, its leaf margins are ciliate, a character absent in the other species. (Note: Over watering bulbs in cultivation inhibits the development of cilia and causes them to become diminutive and inconspicuous – a cultivation aberration.) One other feature is noteworthy: the floral scent of the species is unpleasant, almost putrid, and quite unlike other subgenus *Crinum* species whose floral fragrances are either perfume-like or weakly nondescript. Additional field studies to investigate whether or not flies might be pollinators could prove interesting.

Crinum mauritianum Loddige is a swamp or bog species that is endemic to the salt-water lagoons, marshes, and tidal waterways of southeast Madagascar surrounding the region of Fort Dauphin. I have observed it



Fig. 1. *Crinum xerophilum* cultivated at Parc de Tsimbazaza in Antananarivo, Madagascar, January 15, 1998.

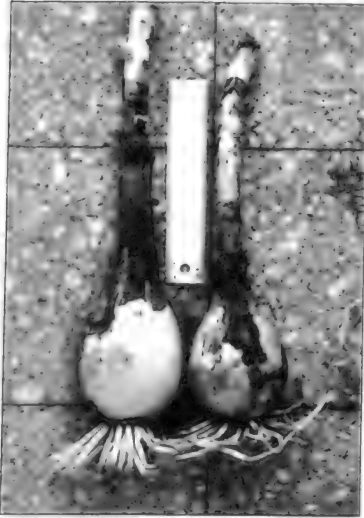


Fig. 2. Bulbs of *Crinum xerophilum* collected at 10km north of Tulear, Madagascar, January 7, 1998. Note the long tapering necks.



Fig. 3. *Crinum xerophilum* collected at 10km north of Tulear, Madagascar, and cultivated in Southeast Texas, September 2001.

All photos by the author.

growing in rocky crevices subjected to ocean wave spray. Bulbs produce abundant numbers of bulky seeds that are buoyant, and little imagination is required to speculate about the possibility of oceanic spread to neighboring islands. This species was attributed to bulbs reputedly originating from Mauritius that Loddige had received via a friend "some years" prior to 1822. However, Mauritius had a well documented history of extensive botanical exploration commencing in 1770 (Baker, 1877), with major floral compilations published by Boyer in 1837 and by Baker in 1877, yet no formal botanical records of a *C. mauritianum* collection existed prior to 1975 (Marais, 1975). Consequently, this species should be regarded as Malagasy in origin. It was collected previously in Madagascar and identified as *C. braunii* Harms (1895) and *C. voyroni* Jumelle (1924-25). How Perrier came to confuse this "salt-water-swamp" species possessing arching, stiff, U-shaped leaves and a leek-like bulb with his "desert" *C. firmifolium* var. *xerophilum* is a complete mystery. Perrier certainly deserves recognition for identifying var. *xerophilum*, but the association with *C. voyroni* must be expunged.

Crinum xerophilum (Perrier) ex Lehmiller, sp. nov. (subgenus *Crinum*).

Species nova a pedicellata umbella et folio ad marginem *C. firmifolium* differt. Type: Madagascar. 2km north of Morombe, March 1972, D.S. Hardy 3568 (Holotype: PRE).

Crinum firmifolium Baker var. *xerophilum* sensu Perrier, in part, excluding reference and observation regarding *C. voyroni* Jumelle. Bulletin de la Société Botanique de France 86:84-92, 1939. Holotype not specified.

Bulb ovoid to oblong with fleshy roots, 7-12 cm in diameter, with a tapering underground neck 19-21cm long, covered with a paper-thin brown tunic of leaf scale; basal offsets seldom produced. Leaves 5-11, forming a rosette, low arching to sprawling on the ground, lorate with most lacking intact apices, ciliate margins with cilia 1-3 mm long, bearing closely spaced longitudinal nerves lacking visible cross striations, containing minute wooly fibers when torn apart, green, 23-86+ cm long, and 4-11 cm wide. Scape often emerging with the leaves, slender, mildly compressed, chartreuse green but sometimes with a faint reddish tint, 10-27cm long; spathe with two bracts, 7.5cm long, bracts reflexed and beginning to wither at anthesis. Umbels 4-15 flowered; flowers actinomorphic, pedicellate with pedicels 10-40mm long, opening at night, unpleasantly scented. Buds slender, light green which gradually fades to a light greenish hue near anthesis, inclining well below the

horizon (but not vertically drooping) before arising to a near erect posture at anthesis. Ovaries shiny green, 5-6 mm long. Perianth tube straight at anthesis, light green, 13-16 cm long. Segments narrow and lanceolate, white with sometimes a greenish tinge to the dorsal outer segments, unequal with the outer segments longer, 55-89 mm long, and 11-12 mm wide, apiculate, the outer segments bearing greenish projections 4mm long. Filaments 6, spreading, white only at the throat, otherwise pinkish purple, unequal with those attached to the inner segments longer, 47-51 mm long; anthers dark at anthesis, pollen golden yellow. Style pinkish purple, 38-80 mm long; stigma weakly capitate. Fruit ovoid to egg shaped, with a smooth surface and bearing an angulated rostellum 75-95 mm long, chartreuse green, 20-40 mm in diameter, indehiscent or pericarp mummifying if very dry conditions; seeds 1-5 per fruit, smooth, pale green, 10-30 mm in diameter.

Habitat: Southwest Madagascar; arid ecology with sporadic summer rainfall pattern often dependent upon tropical storms and typhoons arising in the Indian Ocean. Occurring in sandy soils, ranging from dune sand near the ocean to bushland and spiny forest further inland.

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***PANCRATIUM TENUIFOLIUM* IN THE LIMPOPO RIVER BASIN
OF SOUTH AFRICA'S NORTHERN PROVINCE**

Charles Craib

PO Box 67142, Bryanston 2021, Gauteng, South Africa

Pancratium tenuifolium is at the southern end of its distribution range in South Africa's Northern Province. Although widespread in the Northern Province, the species is rather local according to the limited number of herbarium records. It has been recorded from the arid bushveld north of Thabazimbi to the Phalaborwa area in the east near the Kruger National Park. The records indicate that the plants are found in heavy, dolomitically-derived loam as well as sandy soil. The earliest records are from 1915 to 1936 and the later records from 1969 to 1995. All the records are from the last week in October until the first half of December, with the bulk of records for the month of November.

The Northern Province experiences prolonged and frequent droughts interspersed with substantial rains that fall between November and January. The Limpopo River basin north, northeast and northwest of Ellisras probably has the highest number of amaryllids and the largest diversity of species in various genera of any locality in the Northern Province. These plants have defined flowering periods, flowering either at the beginning of the rainy season between late October and early December, or else in the late summer and early autumn from February to March. If sufficient rains fall in late October and early November, large numbers of plants in populations of various early summer flowering species can be found in flower. The same is true of the late summer and autumn flowering species.

Pancratium tenuifolium is an early summer flowering species. It blooms north of Ellisras in November after soaking rains. It thus conforms to all other records from the Northern Province. Leaves and flowers are produced rapidly after the rain, the process taking as little as two weeks.

The area north of Ellisras is used extensively for cattle ranching and, in recent decades, game farming. This has had different impacts on various *Crinum* species and also on *Pancratium tenuifolium*. The *pancratium* grows either singly or else in clumps of 4-60 bulbs. Clumps of the species are found mostly under dead or very lightly foliated shrubs, and also out in the open. In areas where grazing is heavy, bulbs occur singly or else in clumps of 2-6. The species is locally common in areas with deep sand, but absent from

nearby areas with heavier soils. The species grows together with *Crinum foetidum*, a much sparser plant. The crinum grows singly or else in small groups of 2-3 bulbs, usually with a large mature bulb and 1-2 smaller ones originating from seeds from the parent plant. *Crinum foetidum* sets little seed and flowers sporadically. The seed is easily destroyed by grazing animals. As it does not grow under scrub, it has no protection from trampling.

Clumps of pancratium bulbs flower rather erratically. All bulbs that had flowered in a large population observed on 15 November 2001 were in the process of forming seeds. It seems that despite the extreme brevity of individual flowers they are very attractive to pollinators.

Clumps of pancratium bulbs enlarge from the inside, with the smallest bulbs usually located on the outer perimeter of the clump. Seeds dispersed from parent plants probably obtain the best conditions for germination on the outside of the clump, since the spiral leaves from individual bulbs grow very tightly together and block out sunlight.

The clump-forming habit of this species on moderately grazed sandy soil appears to be related to the fact that seeds can lodge easily and germinate in sand, which retains moisture after rain. In addition, cattle and antelope keep the veld clear from accumulations of moribund grass. Grass cover becomes dense after years of good rain and as fires are much less frequent these days than in earlier decades, grazing animals have a significant function in keeping conditions open. Burning regimes are managed differently from farm to farm, and many are separated by firebreaks. This prevents the vast periodic fires from lightning strikes that occurred naturally in previous decades.

It appears that the pancratium declines when areas become overgrazed. It is probable that populations will recover when grazing pressures ease. This is apparent from the observation of E.E. Galpin made at Mosdene near Naboomspruit. His herbarium collections (National Botanical Institute, Pretoria) made in December 1935 referred to old maize fields that had reverted to savannah grassland housing populations of *P. tenuifolium*.



Figs. 1-3. *Pancratium tenuifolium* near Hoedspruit in the Northern Province, South Africa, growing in open bush veld. Photographs by Maddy Lehman.

***GETHYLLIS LONGISTYLA* FROM THE EASTERN GREAT KAROO AND
GETHYLLIS SPECIES NOVA FROM SOUTHERN NAMAQUALAND**

Charles Craib

PO Box 67142, Bryanston 2021, South Africa

The genus *Gethyllis* contains some very rare species, some only found once or a few times. There are evidently several undescribed species, and these are likely to be narrow endemics or rare as they have not been found before. The description of new *Gethyllis* is made difficult at present as a result of the refusal by two well-known German botanists to return herbarium sheets of *Gethyllis* that were borrowed from the National Botanical Institute in Pretoria.

Gethyllis longistyla is a rare, seldom collected species known from a handful of records from the central and eastern Great Karoo. This region lies in the summer rainfall part of South Africa. Precipitation is often heaviest in the late summer and early autumn from early February to late April. *G. longistyla* is a winter-growing, early summer-flowering species. The growth cycle starts with the beginning of the late summer and autumn rains as the days shorten and ground temperatures cool.

The only recent records are from the foothills of the Sneeuberg and those of the Agter-Sneeuberg in the Murraysburg district of the eastern Great Karoo. In this region the full set of leaves is produced very rapidly after the first good rains between February and late April.

The habitat occupied by the bulbs comprises low dolerite ridges covered in rocks and pebbles, usually with a sparse cover of short grass tufts. The *Gethyllis* are very sparingly distributed, found either in barren areas heavily covered with pebbles or else among grass tufts. The small rosette of leaves is almost cryptic and difficult to spot particularly when covered in wind blown soil or when only the tips of the leaves are visible through silt washed out by heavy rainfall.

The flowering season of this unusual species is rather erratic, usually taking place in November and December. It is not fully understood what brings the plants into flower but this usually coincides with cool overcast weather preceded by heat and soaring early summer temperatures. The bulbs fruit about 9-12 weeks after flowering, usually just before the new season's leaves appear. If the weather is very hot and dry an entire season's crop of seeds will shrivel before they are distributed. It is very rare to find more than a single

bulb, which suggests that the seeds are distributed by animals attracted to the fragrant, fleshy fruit. A number of other *Gethyllis* species form clumps when seeds germinate around the parent bulb.

The best time to take census of bulbs in a given area is when the plants are in flower. One such count of flowering plants over an area of some 15 hectares revealed a population of 12 flowering bulbs.

If the late summer and autumn rains fail the bulbs remain dormant. The winter night temperatures between May and August are cold, frequently well below 0° C. The plants grow actively in the lower autumn temperatures, provided there is moisture, and remain evergreen until September when ground temperatures in the Karoo rise sharply. The leaves shrivel in a matter of a few days and the plants enter dormancy.

The eastern Great Karoo is predominantly a sheep farming area. This has little effect on the numbers of plants. The paucity of plants is not yet well understood but is probably related to erratic flowering and prolonged and frequent drought when the bulbs remain dormant.

Readers of this article are encouraged to make further records should they see plants in the Graaff-Reinet, Victoria West and Beaufort West areas. The rosette of leaves is very distinctive, and the pinkish-lavender flower is strongly scented and very conspicuous. *G. longistyla* is the only *Gethyllis* found in this region, in as far as is known, and this should make the recording process easier.

Namaqualand is particularly rich in *Gethyllis* species. The new species was found on the sandy plains that lie to the south of the Matsikammaberg, a prominent and well-known landmark in Southern Namaqualand close to van Rhynsdorp. The species has one, very occasionally two, oblong pubes-



Fig. 1. *Gethyllis longistyla* in flower among dolerite pebbles in mid-November. Photograph by Carol Knoll.

cent prostrate leaf or leaves. The bulbs grow either singly or in groups of 5-20, but rarely more. The large groups are probably the result of seeds that have fallen around the parent plant. Bulbs grow either out in the open or else within the shelter of thorny scrub.

The growing season starts with the commencement of the first good winter rains which normally fall between early May and early July. The leaves are normally fully developed by mid-July. The plants have only so far been recorded from an area of about 10 square kilometers. They are well represented on one farm but part of the colony there has been ploughed up for a *rooibos* tea field.

The bulbs can very easily be confused with those of a *Strumaria* and, when first found before flowering was observed, were thought likely to be *S. discifera*. The similarity of bulbs in leaf to *Strumaria* will undoubtedly cause problems for adding additional records of this peculiar species should it occur in other parts of Namaqualand.



Fig. 2-3. *Gethyllis species nova* in flower in early December. Photographs by Connel Oosterbroek.

The flowering season appears to be rather early in November. The glistening white flowers are very conspicuous and all emerge from the bulbs within a period of a few days. This gregarious flowering has been observed in a number of *Gethyllis* species.

Although this new species appears to be a narrow endemic, it is well represented at one locality. This is the opposite of *Gethyllis longistyla*, which is usually very sparse at a given locality and absent from a good deal of suitable habitat.

AN UNDESCRIBED *ORNITHOGALUM* FROM SOUTH AFRICA'S NORTH WEST PROVINCE

Charles Craib

PO Box 67142, Bryanston 2021, Gauteng, South Africa

In recent times, efforts have been made to study plants that occupy defined habitats such as cliff faces. The flora associated with sheets of exposed rock has some very interesting adaptations. These areas are periodically both very wet and very dry, and they also experience extremes of heat and cold.

The North West Province is situated in the summer rainfall area of South Africa with most of the rainfall occurring between November and early April. In the Zeerust district where the new *Ornithogalum* occurs, the majority of annual rainfall is usually received between January and March. The habitat consists of open short grassland with sheets of exposed dolomitic rock. The rock sheets have patches of shallow soil. In some areas there are low dolomite hillocks, consisting of almost pure rock. Cracks in the rocks are filled with soil forming an equivalent niche to the pockets of soil that occur on the exposed sheets.

The bulbous flora associated with these rock sheets grows and flowers either in the spring and early summer or in the late summer, autumn and early winter. The temperatures of the rock, fully exposed to daylong sunlight, are too high for growth from mid-November until the end of January. In early February, as the temperatures start to decrease and as the days shorten slightly after the summer equinox, the first few *Ornithogalum* bulbs start to sprout. This process continues until late April with a peak in March, which can be a particularly cool and wet month in the region. The identical signals for the initiation of growth are shared by what may be *Duthiastrum linifolium* that starts to produce its leaves in February. The *ornithogalums* have usually developed their single leaf fully by the onset of autumn in April.

Several species which occur in the same habitat as the *Ornithogalum* flower when the habitat experiences its lowest temperatures and typically highest rainfall, from early February until the end of March. The peak of the flowering period for the *Duthiastrum* is in February and early March. *Nerine frithii*, which occurs in shallow depressions at the edges of the sheets of exposed rock, flowers at the same time. The *Ornithogalum* is most unusual in the timing of its flowering. The bulbs initiate bud development shortly after the winter equinox on 22 June. Fully developed buds are present by the

middle of July. The habitat experiences severe frost between late May and early August. The frosts are usually at their heaviest in July, the main period of bud formation and development.

This undescribed *Ornithogalum* has another peculiar habit. The prominent cluster of striking white flowers is borne at or just above ground level rather like a *Daubenya* or *Massonia* species.

The flowering season lasts from the end of June to the middle of August, with a peak in late July and the beginning of August. Seeds develop rapidly after the plants have finished flowering, from mid- to late August. The dry inflorescence detaches from the bulb and is blown about in the wind, liberating the seeds. Late August and early September are dry and windy at the habitat creating ideal conditions for seed dispersal. Occasionally inflorescences do not detach and seeds are deposited around the parent plant. This set of circumstances explains the occurrence of some of the bulbs in densely packed clusters, where seeds have germinated close together.

Present indications are that the species is a narrow endemic only occurring in an area of about 20 square kilometers. Even within this small area there appears to be much suitable habitat in which the *Ornithogalum* does not occur.

The plants have a great deal of horticultural potential for ornamental pot planting and could form the basis of several cultivars for both the collector and mass market.



Fig. 1. The typical habitat of the new *Ornithogalum* photographed in mid-winter (early July) at the time the plants start to form buds.

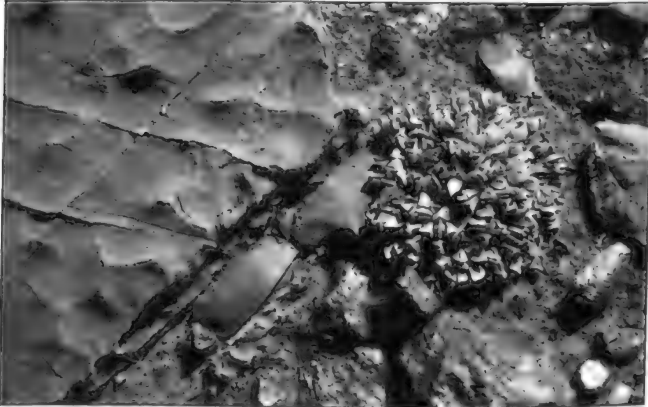


Fig. 2. Habitat photograph of the *Ornithogalum* growing in soil-filled cracks amongst the dolomite rocks. This habitat is also shared with *Rabiea albipuncta*.

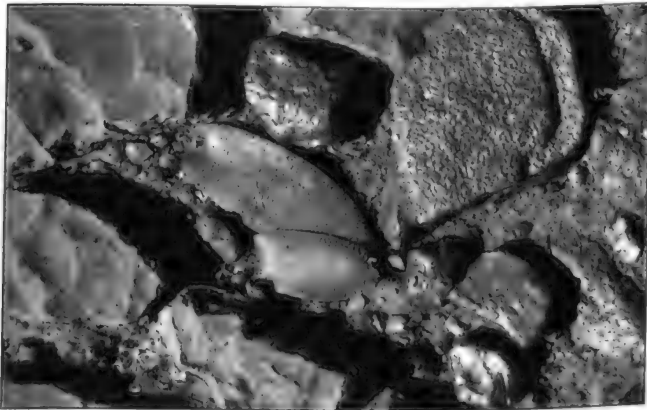


Fig. 3. The leaves are often cryptic amongst the dolomite pebbles particularly when they are covered in dust.

All photographs by Carol Knoll.



Fig. 4. The flowers are produced at ground level or just above it usually as the tips of the leaves start to wither.



Fig. 5. A plant ready to distribute seeds just prior to entering dormancy in September in the dry spring.

PLANT COLLECTING IN THE REPUBLIC OF GEORGIA

Boyce Tankersley

Manager of Living Plant Collections Documentation
Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022

In the spring of 2000, I was fortunate to accompany Galen Gates, Director of Collections at Chicago Botanic Garden and Dr. Susan Wiegrefe, tree breeder from The Morton Arboretum, in a plant collecting scouting trip to the Republic of Georgia sponsored by the Midwest Plant Collecting Collaborative (MWPPC). Dr. Wiegrefe was interested in a number of woody taxa for use in the tree breeding programs at the Morton Arboretum; Galen Gates has a wide interest in plants with emphasis on perennials, and I was the geophyte fanatic.

The MWPPC is a group of botanic gardens and arboreta from the upper Midwest, USA, with common interest in developing collections of plants hardy to this region. The members of this collaborative are the Chicago Botanic Garden (CBG), The Holden Arboretum (THA), Missouri Botanical Garden (MBG), The Morton Arboretum (TMA) and the University of Minnesota Landscape Arboretum (UMLA).

The value of a collecting trip to the Caucasus region of the former Soviet Union (fSU) was strongly supported by Dr. Tatyana Shulkina, former Curator of Living Plants at the Komarov Botanical Institute in St. Petersburg, Russia, and now on the research staff at Missouri Botanical Garden.

The Republic of Georgia (RG), in general terms, occupies a series of valleys bordered on the north by the Greater Caucasus Mountain range (containing the highest peak in Europe) with the Lesser Caucasus Mountain range to the south. Roughly mid-country, a north-south mountain range bisects the Greater Caucasus and Lesser Caucasus Mountains. These mountains, some among the oldest in the world, create innumerable microclimates influenced by the Russian plains to the north, the Black Sea to the west, the Caspian Sea to the east, and the Anatolian Plateau to the south.

The flora of the region represents a crossroads effect. This is the most northern (and hardy) range for taxa representing the Turkish, Iranian and Himalayan floras, and the southern (and most summer heat tolerant) range for taxa from the southern Russia/Ukrainian steppe. Many taxa are elements of the Central Asian floras, and a significant number of taxa centered in RG are elements of the ancient Colchic flora. As a result of these influences, endemism is very high and the Flora of Georgia is very diverse, particularly for herbaceous and geophytic taxa.

Based upon a comprehensive list of Caucasian plants with ornamental potential from Dr. Shulkina, discussion of the merits of a trip lasted 3 years. As part of these discussions, I was asked to research the feasibility of a trip to the Republic of Georgia and/or other countries (Azerbaijan, Armenia, Russian Dagestan) in the Caucasus region. To this end, I spoke with Missouri Botanical Garden research staff that had recently visited Georgia including Mary Merello, Heidi Schmidt, Dr. Jim Solomon and Dr. Nancy Morin. I studied the revised Flora of Georgia (in press), created a Geographic Information System (GIS) comparison of the climate of the Midwest USA and the RG using climatic and soil data supplied by staff at the Institute of Botany, Tbilisi, Republic of Georgia, spent many hours on the Internet collecting information about the language, history and culture of Georgia, confirmed the absence of germplasm from the Caucasus region in any of the living MWPC collections, and arranged for Georgian scientists visiting the herbarium at Missouri Botanical Garden to travel to Chicago to meet other members of the MWPC. Through the efforts of Dr. Shulkina at MBG, Dr. Gia Nakhutsrishvili, the Director of the Institute of Botany, Tbilisi, agreed to issue a formal invitation to MWPC members to visit the Republic of Georgia and participate in scientific endeavors with his staff (an important prerequisite before we could obtain a Georgian visa). Based upon the results of this pre-trip work, a decision was made to proceed contingent on the continued stability of and safety within the country. In recognition of concerns about the lack of an extensive woody flora, a two week scouting trip was authorized to determine the feasibility of a longer trip later in the year to collect woody plant germplasm.

Past plant collecting trips sponsored by MWPC have been planned to take advantage of woody seed and fruit availability in late summer and fall. While researching this trip, I became aware that our plant collections were not only devoid of germplasm from the Caucasus region but were also lacking in spring ephemerals, early summer perennials, and geophytes from known locations.

To facilitate collection of superior germplasm, plant populations would be visited during the peak flowering period (spring and early summer) to locate and tag plants with superior ornamental characteristics in regions with the closest climatic affinities to the Midwestern USA. We were on a tight budget and paid most of the expenses for the trip in advance based upon a detailed estimate of expenses supplied by our host.

In late May, 2000, the members of the team arrived in London for a 32 hour layover on the way to Tbilisi, the only international Georgian airport

with service to the West. While adjusting to the new time zone and purchasing last minute gifts for our hosts, we were fortunate to visit the Chelsea Flower Show and the Royal Botanic Gardens, Kew. Both venues whetted our appetites for new plants.

Collecting in a natural area in Republic of Georgia is similar to collecting in a national park in the USA – plenty of forms/permissions to obtain up front – and a director to approve/disapprove of individual taxa as we found them. In RG all land is held by the state for the use of its citizens in a generic way. Many Georgian nature reserves began as royal Georgian hunting parks that were taken over by the Russian tsars and later the Soviet communists. The biodiversity in these reserves has been undisturbed for hundreds of years.

The transition from Communism to democracy in the Republic of Georgia has not been an easy one. In spite of the hardships, during our visit we were overwhelmed by the warmth, hospitality and generosity of our hosts at the Institute of Botany as well as the Georgian people in general. Under their guidance we collected plants from the valleys to the tops of the mountain ranges (and under their hospitable care we gained weight).

Our first day in Republic of Georgia, we awakened to the sounds of swallows diving outside the balcony overlooking the Trialeti Hills to the west of Tbilisi. Tbilisi is an ancient city, an important crossroad for trade between Asia and Europe, filled with architecture from many periods and cultures, and home to people of many different ethnic and religious beliefs. Early afternoon was spent negotiating with a customs official for the release of supplies shipped by airfreight. After two hours of intense but polite negotiation, our collecting supplies were released. I recommend that future visitors hand carry all items needed. In the RG, all hand carried items are considered “personal baggage” and thus not subject to importation duties (importation duties can run as high as 200%-300% of retail value).

Much of the first day was spent in the Conservation Garden of the Tbilisi Botanic Garden reviewing the work of Dr. Marine Eristavi and discussing the conservation needs of the Caucasus region. Our discussions ranged from potential scientific collaborations to specific plant needs, as well as the need to train new scientists. Restoration of conservation and taxonomy classes at the Institute of Botany for any student from the Caucasus region is a goal of Dr. Eristavi's. Within the protective fences of the Conservation Garden, a number of rare Caucasian plants are grown and their propagation requirements studied. With the fall of Communism, the financial support for educational and research institutions has been prob-

lematic. Despite having received no pay for the previous 18 months, Dr. Eristavi and her staff continue to carry on their important work.

The second day was spent collecting to the southwest of Tbilisi in the Algeti Nature Reserve (41 degrees, 43 min., 55 sec. North Latitude, 44 degrees, 20 min., 53 sec. East Longitude, 1400-1800 m elevation) near Mangliesi, bordering one of the areas of greatest climatic similarity to the Midwest. At Algeti we found an interesting mix of *Quercus macranthera*, *Fagus orientalis*, *Carpinus caucasica*, *Populus tremula*, *Picea orientalis* (naturalized) and *Pinus sosnowskyi* with undergrowth of *Rosa* species, *Polygonatum* and *Primula macrocalyx*. The open glades contained a showy arrays of perennials including *Echium rubrum*, *Orchis caucasica*, *Veronica peduncularis*, *Myosotis* species, *Sedum oppositifolium*, *Hylotelephium caucasicum* and a species of *Orobanch*e. In the higher elevations, we found our first geophyte, *Muscari szovitsianum*, at 1,800 m elevation due north of Mangliesi on a heavily grazed ridge among *Juniperus rufescens*, *Pulsatilla georgica*, *Veronica gentianoides*, *Alchemilla sericata*, *Polygala transcaucasica* and *Androsace barbulata*. Throughout the trip, many of the bulbs we observed were distinctly different from those grown in our gardens, although frequently of taxonomic synonymy. Are the differences we observed due to environment or genetics? By building a documented collection of bulb of wild origin at the Chicago Botanic Garden, we hope to help answer this question.

On the third day, Dr. Wiegrefe and I were deep in the relict forests of the Lagodekhi Reserve in far eastern RG on the flanks of the Greater Caucasus mountain range. In the valley, at 700 m elevation beneath the deciduous canopy of ancient *Fagus orientalis*, *Tilia caucasica*, *Carpinus caucasica*, *Acer pseudoplatanus*, *Corylus avellana*, and *Acer platanoides*, we found ripening seed capsules of *Galanthus lagodechianus* and *Primula woronowii* among *Hedera pastuchovii*, *Erodium cicutarium* and *Urtica dioica*. On a ridge top, 950 m elevation in a rainstorm, Sue found seeds of the rare berberidaceous geophyte, *Gymnospermium smirnovii* (with immense tubers) along an eroding trail with *Primula juliae* and *Dryopteris filix-mas*. In the process of finding an 'almost dry' ford across the rock-laden Ladodekhi River at the end of the day, we found very showy populations of *Scabiosa caucasica*, *Verbascum pyramdatum* and *Leucanthemum* species growing in full sun.

The fourth day was spent visiting the ancient Georgia capital of Mtskheta on the way to the High Mountain Research station at Bakuriani built by the World Wildlife Fund. Bakuriani is located at the southern end of the north-south mountain range that connects the Greater and Lesser Caucasus mountain ranges (41 degrees, 41 min., 13 sec. North Latitude; 43 degrees, 30 min.,

84 sec. East Longitude, elevations from 1,500-2,400 m). It is also an area with close climatic affinities to our Midwest and is known as an area where the elements of several floras overlap. Arriving late in the day, we took a small detour to visit a tenth century Georgian Orthodox church and observed what appeared to be gold-flowered foxtail lilies (*Eremurus* species) on a ledge inaccessible to man (or goat) on the mountainside above the gravel road.

The fifth morning in the field dawned bright and crisp. We piled into the car with Georgian botanists from Tbilisi, Dr. Nukri Sikharulidze (the Field Station director), and our driver and set out to find the elusive *Scilla rosenii*, largest flowered of the hardy squills. We traveled to the south of Bakuriani, climbing a steep gravel mountain road to reach the upper vegetation zones. At the lowest altitude, *Pyrus caucasicus* was in flower not far from the ski lift in the village of Bakuriani. As we traveled up the mountainsides, we encountered *Leucanthemum*, *Pulmonaria* and *Polygonatum* flowering in open woodlands. Near the halfway point, at 2,000 m, we found *Rhododendron caucasicum*, *Betula litwinowii*, *Gentiana dzshimiliensis*, *Sorbus cacausicana*, *Arabis sibirica*, *Gentiana minuta*, *Caltha polypetala*, *Primula pallasii* and *Vaccinium* species with a carpet of *Gagea* species in full flower. Another 100 m higher we stopped for *Macrotoma eichoides* (Boraginaceae), *Muscari sosnowskyi*, *Anemonastrum fasciculatum*, *Pulsatilla violacea*, and *Doronicum longifolium*. At the top of the mountain, 2,400 m, we found the most incredible fields of *Scilla rosenii*, and *Ornithogalum balansae* between rivulets edged with *Caltha polypetala*. The *Scilla rosenii* varied in flower color from deep blue with darker midribs to pure white, and in size from 2.5" to 5" tall. Our Georgian hosts assured us a pink form was also present in the wild populations. Foliage and flower width and thickness were also quite variable. In contrast, the *Ornithogalum balansae* were uniform in all respects.

The sixth day was spent with a VIP tour of the botanic garden associated with the Bakuriani Field Station. *Paeonia lagodechiana*, *Paeonia wittmanniana* and *Iris pumila* were in flower and the *Galanthus* and *Colechicum* had ripe fruit. All of the plants in this garden are of wild origin. Many of the perennials, the peonies, iris and others, as well as the bulbs, are from wild populations. Other specimens, particularly woody plants, are the result of seed collections from natural populations. Using this approach, the Georgian taxonomists can study taxonomic differences between closely related taxa free of environmental variables. The rest of the day was spent pressing herbarium specimens, cleaning seeds and bulbs and packing up for the trip back to Tbilisi.

The seventh day in the field we spent on the road with several significant plant collecting stops. Approximately 5 km north of Bakuriani we stopped to collect a small sample of the vast amount of ripe seed on a population of *Helleborus caucasicus* variable in foliage along the road between Bakuriani and Gori. There are 24 different color forms of hellebores in Georgia and our guides were not sure which population these plants belonged to. The east-facing slope containing the hellebores was pastureland within a pronounced rain shadow, and contained *Pinus kochiana*, *Crataegus* species, *Euphorbia* aff. *myrsinites*, *Berberis* species and *Cerithe glabra*. Across the road and the Jujareti River, agricultural fields filled the valley floor. The west-facing mountain slopes were heavily forested with conifers and mature hardwoods. We were at a confluence of the moisture-laden air from the Black Sea to the West and the drier Eastern climate influenced by Central Asia.

Back in the car, we were off to visit Gori, home of the famous Georgian rose breeder, Iosel Juglishvili, better known by the Russian name he adopted,



Fig. 1. *Iris pumila* at the Bakuriani Botanic Garden.

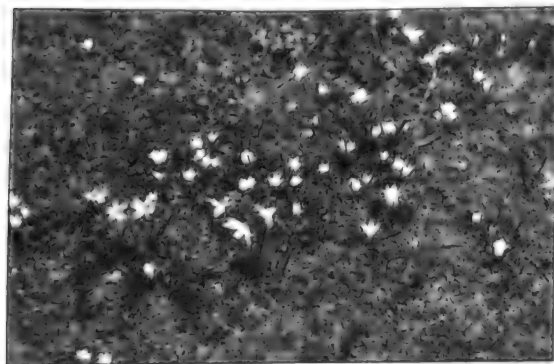


Fig. 2. *Ornithogalum balansae* and *Scilla rosenii* at 2,400 m elevation south of Bakuriani.

Josef Stalin. After a quick inspection of his boyhood home we headed east to the town of Igoeti. Working our way north along dirt roads, we passed many acres of degraded woodlands. The trees and shrubs (*Cornus mas*, *Crataegus* species, *Paliurus spina-christi*, *Ulmus carpinifolia*, *Viburnum lantana*) had sprouted from the base, and the sheep and goats had eaten the apical meristems to produce a thicket of rounded shrubs. Tucked amongst the shrubs wherever sunlight could reach was an amazingly rich herbaceous flora including *Helleborus caucasicus*, *Polygonatum verticillata*, *Dictamnus caucasicus*, *Cerithe glabra* and *Artemisia absinthium*. Further north along the gravel road, we passed wheat fields with the most amazingly brilliant *Consolida divaricata* and *Papaver bracteata* "weeds". The contrast between the gold of the ripe wheat and majestic purple and brilliant red of the "weeds" was awesome; unfortunately, all of the photographs came back under-exposed. We ate a supper packed for us by the staff at Bakuriani on the banks of an irrigation canal in a village famous as the birthplace of the 10th century Georgian poet,



Fig. 3. Field of *Scilla rosenii* at top of pass south of Bakuriani High Mountain Research Station.

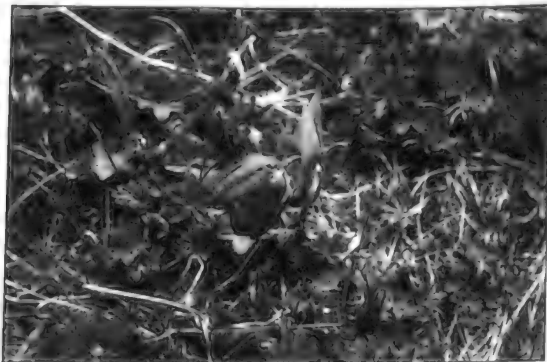


Fig. 4. *Fritillaria latifolia* in the Greater Caucasus Mountains.

Rustaveli. As we ate, each and every farmer and housewife in the village invited us into their home for supper and it was only through the courteous intervention of our driver and field guide that we were able to decline and still avoid any perceived insults to their offers of hospitality. I found it difficult to concentrate while I helped Sue Wiegrefe press the day's herbarium specimens; the water gurgling in the irrigation canal, the adobe homes with red tile roofs, the fragrance of alfalfa at the end of the day and the rustle of the leaves of the *Populus* species in a light breeze all produced a sense of *déjà vu*, evoking the feel of my grandparent's farm in New Mexico half a world away.

Our eighth day in country was spent compiling the list of collected seeds and herbarium specimens as well as cleaning seeds. We had rented a large apartment in Tbilisi for our entire stay and used the space to dry our seeds on newspapers at the end of each day. The apartment owner cooked our meals when we were in Tbilisi and made sack lunches for our day trips. My job was to clean seeds, package them and eventually hand-carry them to the USA and insure they passed inspection at the USDA station at JFK Airport in New York. Sue Wiegrefe had meticulously pressed the herbarium specimens and, with the assistance of our driver, Tamuri, the specimens had been dried each night using a propane heater at the Institute of Botany. After setting the previous day's specimens in the drier, she spent the rest of the day in the Herbarium. Galen Gates spent the day finishing up field notes and confirming arrangements for our departure. That evening, the Director of the Institute, Dr. Gia Nakhutsrishvili, invited everyone to dinner in a restaurant in an outdoor museum of traditional Georgian architecture, located in the hills overlooking Tbilisi. The food, wine and hospitality were excellent.

With our lists submitted for CITES export permits and our seeds and herbarium specimens submitted for phytosanitary inspection, we headed north up the Georgian Military Highway to scout the area around the Kazbegi Field Station, another region with climatic similarities to the Midwest. Kazbegi is situated high up in the Greater Caucasus Mountains near the border with Russia. The road flanks a good-sized river in the foothills with ruins of ancient fortifications on the promontories and ridgelines. The *Rhododendron luteum* were a showy component of the forest understory in the lower elevations and formed one of the few woody components of the highest elevations. Near the crumbling monument to Soviet-Georgian solidarity, the meadows were dotted with *Dactylorhiza euxina* and *Gentiana dzmiliensis*. The gentian was an intense turquoise blue with little if any white in the throat of the flower.

Higher up the road, we found hundreds of *Fritillaria latifolia*, thousands of *Galanthus latifolius* and millions of tiny *Gagea* species in flower not far from the snowline with masses of diminutive pink-flowered *Primula algida* on the streamside banks along with one very rare white-flowered plant. This location exemplified the problem with the theft of bulbs from natural populations that we had only seen traces of previously. Near the road only the tiny and economically worthless *Gagea* were visible. Only after leaving sight of the road did we start to find the first *Fritillaria*. We did not find any *Galanthus* until we crossed a deep, steep-sided stream of ice-cold snowmelt water. On the far side of the stream, we found several piles of rotting *Galanthus* bulbs, apparently abandoned at some earlier time by rustlers. Among the remaining thousands of snowdrops, most of the population were marked with yellow on the flowers. One specimen had flower parts in four's, not three's, as is typical for the genus.

We finished up our day by crossing over a pass onto the north-facing slopes of the Greater Caucasus Mountains. The appearance of the mountains changed subtly from alpine meadows to that of a rock garden. No geophytes were seen but very showy perennials in the genera *Campanula*, *Astragalus*, *Cerastium* and a number of Brassicaceae covered the mountainsides.

Departing Tbilisi, our hosts made sure all our documents were in order and answered the few questions posed by the airport staff. We transited London Heathrow without having to clear British Customs and arrived home the same afternoon.



Fig. 5. Typical plant associations at the Russian border, north side of the Greater Caucasus Mountains.

All photographs by Boyce Tankersley.

As a result of our scouting trip, the MWPCP hired the Institute of Botany to field collect specific populations we observed in flower. The Institute also provided us with propagules of taxa from locations we did not visit during our scouting trip. This relationship has provided the MWPCP with ornamental germplasm while providing the Institute with funds to support a wide range of conservation and taxonomic studies. Georgian scientists visiting CBG in 2001 were given a computer. To date, no plant-collecting trip to the Republic of Georgia has specifically been organized to study the incredibly rich geophytic flora.

LIST OF GEOPHYTIC GERMPLASM RECEIVED

<i>Anemonastrum fasciculatum</i> (L.) Holub.	<i>Iris sibirica</i> L.
<i>Asphodeline lutea</i> (L.) Rehb.	<i>Iris sibirica</i> ssp. <i>elegantissima</i> (no citation found)
<i>Caltha palustris</i> L.	<i>Leucojum aestivum</i> L.
<i>Colchicum speciosum</i> Steven.	<i>Lilium georgicum</i> Mandem.
<i>Crocus adamii</i> J. Gay	<i>Lilium monadelphum</i> Bieb.
<i>Crocus sharojanii</i> Rupr.	<i>Lilium szovitsianum</i> Fisch. & Ave-Lall.
<i>Crocus vallicola</i> Herb.	<i>Merendera trygyna</i> (Adams) Stapf.
<i>Erythronium caucasicum</i> Woronow.	<i>Muscari sosnowskyi</i> Schschian
<i>Fritillaria caucasica</i> Adams.	<i>Muscari szovitisianum</i> Bak.
<i>Fritillaria latifolia</i> Willd.	<i>Muscari tenuifolium</i> Tausch.
<i>Fritillaria lutea</i> Bieb. non Mill.	<i>Ornithogalum balansae</i> Boiss.
<i>Galanthus caucasicus</i> (Bak.) Grossh.	<i>Ornithogalum kochii</i> Parl.
<i>Galanthus lagodechianus</i> Kem.-Nat.	<i>Pancratium maritimum</i> L.
<i>Galanthus latifolius</i> Rupr. non Salisb.	<i>Polygonatum verticillatum</i> (L.) All.
<i>Galanthus woronowii</i> A. Los.	<i>Pulsatilla georgica</i> Rupr.
<i>Gladiolus kotschyanus</i> Boiss.	<i>Pulsatilla violacea</i> Rupr.
<i>Gladiolus tenuis</i> M. Bieb.	<i>Scilla rosenii</i> C. Koch.
<i>Gymnospermium smirnowii</i> (Traub.) Takht.	<i>Scilla sibirica</i> ssp. <i>caucasica</i> (no citation found)
<i>Iris caucasica</i> Hoffm.	<i>Sternbergia fischeriana</i> (Herb.) Rupr.
<i>Iris colchica</i> Kem.-Nat.	<i>Sternbergia lutea</i> (L.) Spreng.
<i>Iris iberica</i> Hoffm.	<i>Tulipa cichleri</i> Reg.
<i>Iris iberica</i> ssp. <i>elegantissima</i> (Sosn.) Fed. & Takht.	<i>Tulipa julia</i> K. Koch.
<i>Iris pumila</i> L.	<i>Tulipa karabachensis</i> Grossh.
<i>Iris reticulata</i> Bieb.	

A CLOSER LOOK AT *GRIFFINIA ESPIRITENSIS* RAV.
(AMARYLLIDACEAE)¹

Kevin D. Preuss² and Alan W. Meerow¹

¹1932 20th Ave N., St. Petersburg, FL 33713

²USDA-ARS-SHRS, National Germplasm Repository
13601 Old Cutler Rd., Miami, FL 33158

ABSTRACT

Griffinia espiritensis Ravenna was described from a population near the Sooretama Biological Reserve in the state of Espírito Santo, Brazil. This species, which ranges north into the state of Bahia, is found only in Coastal Atlantic Rain Forest (Mata Atlântica), and is the most morphologically diverse of the genus. Two varieties are described from Bahia, *G. espiritensis* var. *ituberae* and *G. espiritensis* var. *baiana*. Several recently described species of *Griffinia* are relegated to synonymy with *G. espiritensis*.

One of about fifteen species in the genus *Griffinia* Ker Gawl. (Amaryllidaceae), *G. espiritensis* Rav. was described from the Brazilian state of Espírito Santo (Ravenna, 1969). Recent collections indicate a more northern and western distribution of this species (Preuss 1999a, 1999b; Ravenna 2000). The broad range of distribution for *G. espiritensis* overlaps with *G. parviflora* Ker Gawl., *G. arifolia* Rav., *G. liboniana* Morren, *G. aracensis* Rav., and *G. intermedia* Lind. (synonym: *G. ilheusiana* Rav.) in southern Bahia, the putative center of diversity for the small, blue-flowered *Griffinia* species. Unfortunately, much of the primary growth forests necessary to support *Griffinia* populations no longer exist in southern Bahia.

Located about 30 km west of the municipality of Ituberá, Bahia, Fazenda Piauí, with more than 700 hectares of old growth forest, has yielded two different forms of *Griffinia* that have been assigned to the *G. espiritensis* group. A collection from near Belmonte, Bahia, just east of the Serra do Mar near Rio Jequitinhonha, represents yet another form of *G. espiritensis* Rav. (Preuss 1999a), and is considered here distinct. Several other collections verify the occurrence of *G. espiritensis* in southern Bahia.

Griffinia espiritensis Rav. *Pl. Life*, 25: 67. 1969. TYPE: BRAZIL, Espírito Santo, Sooretama Biological Reserve, on the way to the waterfall, Dec 1965, *P. Ravenna* 399 (Holotype: Herb. Ravennae).

¹ This paper was peer-reviewed before publication.

Bulb 2–8 cm. in diam.; neck to ca. 2 cm. long. Leaves elliptic-lanceolate (-ovate), acute, arcuate or patent, lamina 7–22 (-32) cm. long and 4–8 cm. broad, entire, straight to undulate, solid green or variously maculated whitish; petiole ca. 2–20 (-28) cm. long. Scape from 9–38 cm. tall, two-edged; spathe bracts 2, 1.5–2.5 cm. long and 3–9 mm. broad at base, obovolute, broadly lanceolate, fused basally and overlapping on one side; pedicels ca. 0.8–1.5 cm. long; umbel 4–10 flowered. Perianth epigynous, horizontal, perigone cornute, hypanthium lacking; perigone to 3.3 cm long; tube ca. 1–3 mm long, green at the base changing to white then lilac distally; tepals various shades of lilac with white in the center, tepal segments oblanceolate obtuse to obovate acute, the upper 5 straight or reflexed, the upper the longest and broadest, the lower shortest and narrowest, more or less straight and revolute, the outer whorl of tepals apiculate. Androecium of (5-) 6 stamens (5+1), of various length from ca. 11–29 mm. long, five declinate, the upper one assurgent or suppressed; filaments pale lilac-white; anthers oblong, ca. 2–3 mm. long; pollen greyish-white. Gynoecium comprised of a filiform, simple style 2–3.3 cm long, subequal in length to the tepals; stigma capitate, rarely trilobed to trifid; ovary 4–7 mm long and 3–5 mm in diam., trilocular, green, ovules 4–10 per locule. Fruit, ca. 16–21 mm long and 10–15 mm diam., subglobose-ovoid; seeds typically 1–3(6), ca. 5–8 mm diam., globose, turgid, white or greenish-white. Chromosome number $2n = 20, 30$.

Griffinia espiritensis Rav. var. *espiritensis* (Fig. 1C & 1D.)

Bulb ca. 5 cm. Leaves arcuate; lamina 12–22 cm long, 7–8 cm broad, elliptic, entire, variously speckled; petiole 15–28 cm long. Scape to 38 cm long. Inflorescence 5–10 flowered; pedicels 1.0–1.5 cm long. Perigone pale lilac, cornute, 3.0–3.3 cm long, tube 2–3 mm long; tepals elliptic, slightly reflexed, margins straight. Stamens 5 or 6, two ranked, 18–29 cm long. Style 2.6–3.2 cm long, punctate-capitate. Ovary 6–7 mm long, ca 5 cm diam., 6–8 ovules per locule. Fruit, to ca. 20 mm long, to 15 mm diam., nodding, and 1–3 seeds per capsule; seeds globose, ca. 7– mm diam. Chromosome number $2n = 30$.

SPECIMENS EXAMINED: BRAZIL: Espírito Santo, Rod. BR-101, 20 km S de Linhares, 16 Oct 1983 G. Hatchbach & O. Guimarães 46913 (US); Espírito Santo, in cult. at Univ. of FL, March 1995; Bahia, Ituberá, cultivated by J. Silva dos Santos, June 2, 1997.

Both forms of *G. espiritensis* var. *espiritensis* investigated were found to have the chromosome number of $2n = 30$. However, both were cultivated forms extirpated from local populations. The leaves of this variety are

remotely speckled. Unlike the other varieties of *G. espiritensis*, *G. espiritensis* var. *espiritensis* has a tall peduncle, long petioles and leaves that tend to be a darker shade of green. This variety is the most prolifically offsetting form of the species.

Griffinia espiritensis Rav. var. *ituberae* K. Preuss & A. Meerow, var. nov. (Fig. 1A & 1B.). TYPE: BRASIL. Itubera, Bahia, Fazenda Piaui, BR km 28, occurring in the wet understory of primary growth forest of the Serra do Mar, near the banks of a stream, ca. 300 m alt. March 1995, Lima s.n., (FLAS).



A



B



C

Fig. 1. Floral variation found in *Griffinia espiritensis* Rav. A. *Griffinia espiritensis* var. *ituberae*, $2n = 30$. B. *Griffinia espiritensis* var. *ituberae*, $2n = 20$. C. *Griffinia espiritensis* var. *espiritensis*, $2n = 30$. D. *Griffinia espiritensis* var. *espiritensis* 'Santos', $2n = 30$. E. *Griffinia espiritensis* var. *baiana*, $2n = 20$. Photographs by Kevin D. Preuss.



D



E

Griffinia espiritensis var. *ituberae* ab ea statura robustas, scapo validior, floribus amplioribus, brevioribus, vividibus lilacinibus colore et cum albo ad instar stellae, foliis patentibus, latior foliis, crassior petiolus. Habitat in silvis primariis Matae Atlanticae, crescit in umbra funda.

Plant to ca. 26 cm tall. Bulb ca. 7-8 cm diam., subglobose, with a short pseudoneck to 1 cm long; rhizomes producing bulbils. Leaves spreading; lamina 15-22 cm long, 5-7 cm wide, elliptic (rarely ovate), variously speckled whitish, petiole 4-11 cm long and 1-1.5 mm in diameter. Inflorescence, 6-11-flowered; scape to 22 cm tall, spathe bracts 1.8-2.3 cm long; pedicels 1-1.5 cm long. Perigone lilac with white in the center forming a stellate pattern; cornute, tube 2-3 mm long, 3 mm in diameter, the uppermost tepal ascending, to 2.8-2.9 cm long, ca. 7.5 mm wide, two ascending tepals each ca. 2.7 cm long 6 mm wide, the lateral two 2.8 cm long 7 mm wide, and the lowermost descending, ca. 2.75 cm long, ca. 3-4 mm wide, revolute, obovate to elliptic, apiculate, apicules ca. 3 mm long. Stamens 5 or 6, of unequal lengths, 2.1 cm, 2.0 cm, 1.5 cm 1.4 cm, 1.2 cm, and 1.5 cm (when present), 5 declinate and 1 assurgent (when present), adnate to tube; filaments lilac-white; anthers 3 mm long, lavender; pollen dirty white. Ovary ca. 6 mm long, ca. 5 mm in diameter, oblong.; 6-8 globose ovules per locule; style 2.2-2.8 cm long, stigma 1mm broad, punctate (-capitate). Fruit nodding; seeds 1-6, globose. Karyology $2n = 20, 30$.

OTHER SPECIMENS EXAMINED: BRAZIL; Bahia, Fazenda Piauí, approx. 30 km west of the municipal of Ituberá, along a fencerow in deep shade. Coll. 28 May, 1997, Preuss 104. (FLAS).

Plants of *G. espiritensis* var. *ituberae* were sent to us from fazenda Piauí, located in the Mata Atlantica's Serra do Mar about 30 km west of the municipal Ituberá, Bahia. *Griffinia espiritensis* var. *ituberae* occurs in deep shade of the tropical primary growth forests. *Griffinia espiritensis* var. *espiritensis*, known from the state of Espírito Santo, and *G. espiritensis* var. *ituberae* are allopatric and now biogeographically isolated from one another in the once contiguous Atlantic forest, via mesophytic and dystrophic forests (caatinga and restinga) and deforested regions of southern Bahia.

Griffinia espiritensis var. *ituberae* differs morphologically from *G. espiritensis* var. *espiritensis* by its stout, but robust stature, smaller flowers, which are deeper lilac in color and contrasted by a white stellate pattern in the center of the perigone. Stigma morphology in these two varieties is punctate - not obscurely tri-lobed, as in *G. espiritensis* var. *baiana*. There is considerable variation found within the two forms of *G. espiritensis* var.

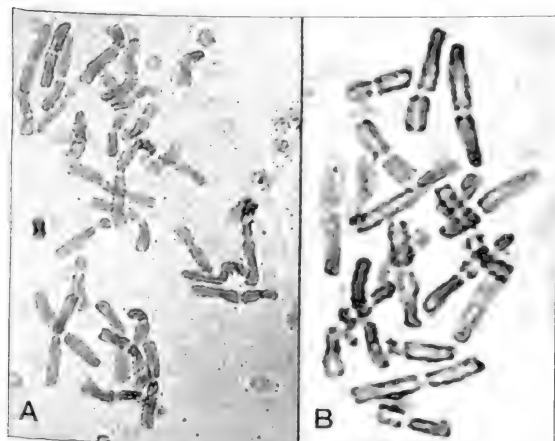


Fig. 2. Chromosomes of the two forms of *Griffinia espiritensis* var. *ituberae*. A. $2n = 30$. B. $2n = 20$.

ituberae. The first accession acquired by Meerow proved to be triploid, while the second accession acquired by Preuss was diploid (Fig. 2). The $2n = 20$ forms (Fig. 1B) are overall smaller plants with flowers of a different form; the tepals are narrow with acute, not obtuse apices, and deeper lilac in color. Based on nuclear ribosomal DNA

ITS sequences the three diploid individuals were identical to that of the triploid individuals (Preuss, 1999a).

Griffinia espiritensis Rav. var. *baiana* Preuss & Meerow, var. nov. (Fig. 1E).

TYPE: BRAZIL. Bahia, Belmonte: east of the Serra do Mar near the banks of Rio Jequitinhonha in the understory of an old cacau grove, alt. ca. 50 m., 9 Nov 1997, Preuss 110 (FLAS).

Griffinia espiritensis var. *espiritensis* Rav. et *Griffinia espiritensis* var. *baiana*. affinis sed robustus minore, floribus paucioribus, brevioribus, vividibus lilacinibus in coloribus et cum albo ad instar stellae, tepalis undulatis post anthesin, foliis arcuatis, tenuiorfolibus, petiolus graciliore, lamina basi sensim in petiolum attenuata, lamina magis lanceolati et immaculati. Chromosomatorum numerus $2n = 20$. Habitat in sylvis, crescit in umbra funda, praesertim prope rivulos.

Plant 11 – 19 cm tall. Bulb ca. 3 cm diam. Leaves arching; lamina 7 – 10 cm long, 2 – 4 cm wide, lanceolate, non-speckled, petiole 5 – 11 cm long and ca. 5 – 6 mm in diameter. Inflorescence 4–6-flowered; scape 9 – 16 cm tall, ca. 3–5 mm in diameter; spathe bracts ca. 15 mm long, 3 – 4 mm wide at base; pedicels 8 – 10 mm long, ca. 2 mm in diameter. Perigone deep lilac in color with white in the center, horizontal; cernuous; tube ca. 1 mm long and 2 mm in diameter, the uppermost tepal ascending, 2.8 – 3 cm long 4 mm wide, two ascending tepals each 2.7 – 2.8 cm long, ca. 3 mm wide, the lateral two 2.6 cm long, 3 mm wide, the lowermost 2.5 cm long, ca. 2.5 mm wide descending, revolute, apicules ca. 2 mm long, tepal segments elliptic, undulate after anthesis. Stamens 5 or 6, of unequal lengths, 2.3 cm, 2.4 cm,

1.9 cm 1.8 cm, 1.6 cm, and, 1.5 cm (when present), 5 declinate and 1 assurgent (when present), adnate at base. Ovary, 5 – 6 mm long, 4 mm in diameter, oblong; 4–8 ovules per locule, globose; style ca. 2.7 cm long, filiform, declinate, stigma punctate, rarely trilobed to trifid. Fruit nodding; seeds 1–3, globose. Chromosome number $2n = 20$.

A small cluster of a few plants (presumably clones) were found growing in an old, abandoned, heavily shaded grove of *Theobroma cacao*, in close proximity to the banks of Rio Jequitinhonha near Belmonte, Bahia, just east of the Serra do Mar (Preuss 1999a). Plants most similar to those located near Belmonte were also found in cultivation in Bahia. This variety is morphologically similar to *G. itambensis* Rav. but the flowers are larger with a white stellate pattern in the center and the tepal margins are undulate. *Griffinia espiritensis* var. *baiana* is the smallest form of *G. espiritensis* and differs from *G. espiritensis* var. *espiritensis* by reduction in floral number to 4–5(–6), smaller flowers, shorter floral tube, delicate leaf with lamina that lacks spotting, and undulate tepals. Another character that can be observed upon anthesis is a white stellate pattern contrasting the bright, undulate, lilac tepals. *Griffinia espiritensis* var. *baiana* differs from both *G. espiritensis* var. *espiritensis* and *G. espiritensis* var. *ituberae* by its smaller size, reduction in floral number, shorter perigonal tube, reflexed, undulate tepals, narrow lanceolate lamina that lack spotting, and tri-lobed stigma.

It is evident that the morphology of *G. espiritensis* is highly variable throughout its range. The tepals vary from linear, undulate and reflexed in *G. espiritensis* var. *baiana*, to obovate, entire and not reflexed in *G. espiritensis* var. *ituberae*. The leaves may have long or short petioles. The lamina may be lanceolate (*G. espiritensis* var. *baiana*) or occasionally broadly elliptic, rarely ovate. Like *G. liboniana* and *G. aracensis* Rav., forms of *G. espiritensis* have spotted laminae, but usually to a lesser extent than *G. liboniana*. With the exception of *G. espiritensis* var. *baiana*, the laminae are variously speckled whitish. The degree of leaf speckling is quite variable and inconsistent. The origin of this character is uncertain. Among individuals of the diploid form of *G. espiritensis* var. *ituberae*, leaf maculation varies from lacking to profuse; the triploid form only remotely expresses the trait. An individual plant may demonstrate spotted laminae during one season and not another. The triploid forms of *G. espiritensis* are larger and more robust than the diploid forms investigated.

All varieties of *G. espiritensis* exhibit the floral features characteristic of the *G. liboniana* complex within subgenus *Griffinia*: diurnal, unscented,

lilac-colored flowers, insertion of floral parts to the top of the ovary (epigynous), strongly zygomorphic perianth (5+1) with the stamens arranged in a pattern of 5+1 (i.e. 5 declinate and 1 assurgent), often with the assurgent stamen suppressed, and increased number of ovules (Preuss 1999a, 1999b). Recognition of these three varieties under a broader circumscription of *Griffinia espiritensis* more accurately reflects the evolution of this species (Fig. 3b). *Griffinia itambensis* Rav. is quite possibly a variant of *G. espiritensis* with a more western distribution. Unfortunately, attempts to extract DNA were unsuccessful (Preuss, 1999a).

Based upon the localities and descriptions, Ravenna's newly described species, *G. paubrasilica*, *G. mucurina*, and *G. colatinensis* are most likely mere varieties of *G. espiritensis*. All three species occur in the range of *G. espiritensis*. *Griffinia paubrasilica* Rav., from Itamarajú, Bahia (Ravenna, 2000), which Ravenna compares to *G. liboniana* Morren, is a spotted-leaf form of *G. espiritensis* var. *ituberae*. When visiting the herbarium at CEPLAC (Itabuna, Bahia), the first author had determined the specimen (*Hatschbach* 53647) from Itamarajú, Bahia to be *G. espiritensis*. *Griffinia mucurina* Rav. is also thought to be another form of *G. espiritensis*. Ravenna (2000) himself states "*Griffinia mucurina* appears closely related to *G. espiritensis*... Actually, the leaves are indistinguishable, but in the latter species perigone is much smaller." On the basis of the locality and description of another newly described taxon (Ravenna, 2000), *G. colatinensis* Rav., another variant of *G. espiritensis* may have been unnecessarily recognized at specific rank. Additional DNA studies might elucidate the exact relationships of these new taxa more precisely.

REPRODUCTIVE BIOLOGY

Species of *Griffinia* reproduce asexually by daughter bulbs emanating from the basal plate, however, some forms of *G. espiritensis* also produce bulbils on rhizome-like structures. On two occasions, the author has observed up to seven and eight bulbils on a rhizome segment. As far as is known in the genus, this phenomenon occurs only in this species. All forms of *G. espiritensis* examined so far do not show any signs of self-compatibility. Attempts to cross the two triploid forms of *G. espiritensis* var. *espiritensis* and the triploid form of *G. espiritensis* var. *ituberae* have demonstrated that they are inter-fertile. *Griffinia espiritensis* var. *baiana* and the diploid form of *G. espiritensis* var. *ituberae* examined also appear to be inter-fertile. Crosses involving *Griffinia espiritensis* var. *baiana* and *G. espiritensis* var.

espiritensis have demonstrated inter-fertility as well. When crosses were attempted between the triploid and diploid forms of *G. espiritensis* var. *ituberae*, no seed was produced.

Pollination biology of *Griffinia* has not yet been investigated. Pollen fertility was examined in some taxa of the small, blue-flowered *Griffinia* (Preuss, 1999a). The protocol used was shown to be effective for the differential staining of aborted and non-aborted pollen in *Amaryllis* (Alexander, 1969). Differential staining of viable and nonviable pollen was conducted to discern the influence of $2n = 30$ and $2n = 30$ on the levels of pollen fertility of the corresponding taxa (Table 1). There was no direct correlation between the diploid and triploid forms of *G. espiritensis* and fertility.

Table 1. Pollen viability percentages and chromosome numbers of *Griffinia espiritensis*.

Taxon Number	Pollen viability	Chromosome
<i>Griffinia espiritensis</i> var. <i>espiritensis</i> (Espirito Santo)	93 %	$2n = 30$
<i>G. espiritensis</i> var. <i>espiritensis</i> (Bahia)	54%	$2n = 30$
<i>G. espiritensis</i> var. <i>ituberae</i>	67%	$2n = 30$
<i>G. espiritensis</i> var. <i>ituberae</i>	99.5 %	$2n = 20$
<i>G. espiritensis</i> var. <i>baiana</i>	68%	$2n = 20$

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TWO NEW WHITE-FLOWERED *GRIFFINIA* SPECIES¹

Kevin D. Preuss² and Alan W. Meerow¹

²1932 20th Ave N., St. Petersburg, FL 33713

¹USDA-ARS-SHRS, National Germplasm Repository,
13601 Old Cutler Rd., Miami, FL 33158

ABSTRACT

Griffinia leucantha and *G. cordata*, distinct from any other known species of the genus, are described as new from nineteenth century herbarium specimens. Both belong to subg. *Griffinia*. These Brazilian species lack blue range pigments in the flowers, a characteristic of *Griffinia* subg. *Hyline*, but share the derived characters (e.g. several flowers per scape, few ovules per locule, 5 + 1 staminal arrangement) of *Griffinia* subg. *Griffinia*. Both *G. cordata* and *G. leucantha* have stout scapes and white flowers; however, the perianth is epiperigynous in *G. cordata* and epigynous in *G. leucantha*. In stature, *G. cordata* is intermediate between *G. alba*, another white-flowered species, and *G. leucantha*, but unlike those species it has strikingly cordate leaves.

Griffinia, a critically endangered Brazilian genus, is one of two members of the Neotropical tribe Griffineae (Meerow et al., 2000). *Griffinia* are highly prized horticulturally for their blue flowers. White flowers were previously thought to be restricted to *G.* subg. *Hyline* (Ravenna, 1969), until the recent description of *G. alba* K. Preuss and Meerow (2000). Species of subg. *Hyline* have only 2-3 large, crepuscular and ephemeral, fragrant, white flowers per scape. The six stamens are declinate, and there are numerous ovules per locule. Plants of subgenus *Griffinia* have several to many lilac and/or white flowers, and stamens arranged in a 5 + 1 manner, five declinate and one assurgent (the latter sometimes obsolete) and few ovules per locule. Flowers of subg. *Griffinia* are never fragrant. We believe that two *Griffinia* specimens collected by Sanders in 1892 from Brazil and deposited at the Royal Botanic Gardens, Kew Herbarium each represent an undescribed species of white-flowered *Griffinia*.

Key to the new species of *Griffinia*:

1. Scape 2-3 - flowered; flowers white, perigone 15-18 cm long, crepuscular, fragrant; stamen six in three ranks of two, declinate, resting on the lowermost tepal, pollen yellow; ovules 10-16 per locule
.....Subgenus *HYLINE*

¹ This paper was peer-reviewed before publication.

1. Scape 5-20 - flowered; flowers blue, lilac and/or white, perigone 2-12 cm long, diurnal, lacking scent; stamen five or six, five declinate, one assurgent or suppressed, pollen white; ovules 2-8 per locule2 (subg. *GRIFFINIA*)
2. Leaves oblong, attenuate at the base, adaxial surface of petiole channeled; 10-12 flowers white, perigone about 3 cm long, tepals less than 4mm wide*Griffinia leucantha*
2. Leaves orbicular, cordate at the base, adaxial surface of petiole flat; 9-11 flowers white, perigone about 4 cm long, tepals more than 4 mm wide*Griffinia cordata*

Griffinia leucantha K. Preuss, sp. nov.

TYPE: BRAZIL. 12 Sept. 1892. *F. Sanders et al* s.n. (holotype, KEW).

Species nova *G. cordata* affinis sed ab ea foliis oblongatis, petiolis brevioris, pedunculo robustiore, corolla brevioris.

Bulb globose, ca. 5 cm diam.; tunics brown. Leaves oblong, obtuse, to 29 cm long, narrowed gradually to a broad, adaxially channeled petiole about 15 cm long. Peduncle thick, short, ca. 11 cm tall, compressed. Umbel 10-12 - flowered, pedicels 1.4 - 2.0 cm long. Perigone white; tube short, 1-2 mm long, not continuous with the pericarp; tepals 2.8 - 3.2 cm long.. Stamens 6 (5 declinate and 1 assurgent), 1.7 - 3.0 cm long, white; anthers small, oblong, versatile. Ovary oblong 12-14 mm long, bright green, ovules 2 per locule, style simple, 3.0 cm long, stigma punctate.



Fig. 1. Holotype of *Griffinia leucantha* (*F. Sanders* s.n., KEW).



Fig. 2. Holotype of *Griffinia cordata* (*F. Sanders* 280, KEW).

This Sanders collection (K) is without number or locality, but was collected on September 12, 1892. The specimen consists of just a 10-flowered scape. A note indicates that there is a painting of the plant in the "Drawings Collection". According to Sanders, this species of *Griffinia* is described as having "peduncle very thick, short, compressed; umbel 10-12-flowered, pedicels short; ovary 1/2 in. long, bright green...". In conjunction with white flowers, this combination of characters is unique to *G. leucantha*. Sanders describes the leaves as "bright green, oblong, obtuse, nearly 1 ft. in length, narrowed gradually to a broad, channeled petiole 1/2 ft. long...", characters most similar to *G. intermedia*, another poorly understood species. *Griffinia leucantha* is similar to *G. intermedia* Lind. and *G. cordata* K. Preuss in stature. However, *G. intermedia* has blue, epiperigynous flowers. Like *G. cordata*, *G. leucantha* has a robust scape with purely white flowers. *Griffinia leucantha* has oblong leaves, short pedicels, and epigynous flowers, an important character of the species in the *G. liboniana* complex (Preuss, 1999). Perhaps the painting would depict the presence or absence of reddish pigmentation in the petioles and scape, a character unique to the epiperigynous taxa (Preuss, 1999).

Griffinia cordata K. Preuss and A. W. Meerow, sp. nov.

TYPE: BRAZIL. Sanders 280, 1892. (holotype, KEW).

Species nova *G. leucantha* affinis, sed ab ea foliis cordatis, petiolis crassioris, pedunculo longiore, pedicels longiore, corolla longiore.

Bulb, not seen. Leaves orbicular, petiole 12-13 cm long, round abaxially, flat adaxially, lamina ca. 18 cm long, 14 cm wide, cordate bases and mucronulate apices. Peduncle 9-17 cm tall; umbel 9-11-flowered; pedicels 1.3-2.5 cm long; flowers epiperigynous. Perigone white, ca. 4 cm long, tube 4-6 mm long, continuous with the pericarp, tepals 3.1-3.6 cm long and 4-6 cm broad, Stamens 6, five declinate 1.9-2.8 cm long, one assurgent ca. 2.6 cm long. Style ca. 3.0 cm long, stigma punctate. Capsule subglobose, 23-25 mm long and 20-24 mm broad.

This type of *G. cordata* lacks collection information, but shows the leaf and the peduncle in both flowering and fruiting condition. *G. cordata* is similar to *G. alba* in flower size, form and color, but is smaller in stature, and bears fewer flowers on a stouter scape. The cordate leaves are unique in the genus. *G. cordata* has similar flower number and peduncle morphology to *G. leucantha*, but differs by its cordate leaf base and larger flowers on long pedicels. Additionally, this new species has epiperigynous flowers, a condi-

tion in which the tepals and stamens are attached to the floral tube or hypanthium cup above the ovary with the lower part of the hypanthium adnate to the ovary (Radford et al., 1974). This is a character shared with *G. hyacinthina* Ker Gawl., *G. intermedia*, *G. parviflora*, and *G. alba*.

As is common with several of the nineteenth century collections of *Griffinia*, locality and collection data for these specimens are incomplete or even lacking. Although such essential information is incomplete, these two species are notably different from any other described species of *Griffinia*. It is uncertain if populations of these two species still naturally occur or even if these plants might be found in cultivation in Brazilian gardens. Details about the ecology of these two species could provide some further insight into the evolutionary significance of white flowers and the phylogenetic position of these two species in the genus *Griffinia*.

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BOOK REVIEW

Snowdrops. A monograph of cultivated *Galanthus*. Matt Bishop, Aaron Davis and John Grimshaw. The Griffin Press, 35 Wessex Way, Cox Green, Maidenhead SL6 3BP, UK. Hardcover 363 pp, many colour photographs, \$63.65. ISBN 0 9541916 0 9. 2001.

When it comes to collecting minutiae in the plant world, *Galanthophiles*, as they have become known, must take one of the top prizes. Every tiny nuance of shape and markings is deemed to be sufficient to name another new cultivar and over 500 of them are recognized in the present volume—but I use the word ‘recognized’ with tongue in cheek. The mischievous would say that if those 500 snowdrops were planted together in a plot and then the labels removed, no one would ever be able to put them back in the right places! However, armed with this new book, one does stand a sporting chance of identifying some of them correctly. In a way, that there should be so many selections is at first surprising, for *Galanthus* is a small genus of only about 20 species and the differences between them are not strikingly obvious at a glance. Among the non-converts the comment ‘they all look alike’ is heard not infrequently and one has to admit that they do all have the same basic flower structure—the familiar pendent white flowers with the three outer segments larger than the three green-blotched inner ones. However, it is the size and shape of these green blotches, coupled with leaf veneration (the way in which they are folded together in the young stages), leaf width and colour (green versus glaucous) that provide the taxonomist and gardener with the tools of their trade. So it is, that the enthusiast will go on and on selecting slight variations which, having acquired clonal names, will command considerable prices at the increasingly frequent snowdrop events around the UK countryside.

This substantial and well-illustrated book begins with a detailed description of the snowdrop plant, followed by a chapter on the wild species by Aaron Davis whose *Botanical Magazine Monograph* of *Galanthus* preceded this in 1999. This section gives much the same information as before, but is updated to include new observations and taxa such as the recently described *G. trojanus*. The main bulk of the book is devoted to the cultivars, and there has been a valiant attempt to classify these, firstly based upon the type of leaf veneration and then on fairly easily observed features of the flowers. For example, in Chapter 4, cultivars of species with applanate veneration, we find the cultivars of *G. nivalis* divided into 4 groups: those with a single apical

green V or U on the inner segments, those with a similar but yellow mark, those without any marks at all, and those in which the outer segments have a green mark; these groups are subdivided on a range of other characters such as leaf colour, spathe modifications, ovary colour, etc. It is a complicated layout, but there are lettered/numbered keys that help users to find their way around. The cultivars of each species are dealt with in this way, followed by hybrid cultivars, which are split into two chapters describing the normal single ones and then the 'doubles', i.e. those with many more segments than usual. A substantial chapter on cultivation is followed by the interesting Chapter 11 providing mini-biographies of well-known Galanthophiles of the past, for example, James Allen, E. B. Anderson, Samuel Arnott, Lady Beatrix Stanley, Primrose Warburg and so on. Recommended places to see snowdrops, a very extensive bibliography and the index end this comprehensive volume. I find the index not very user-friendly in that the cultivars are listed alphabetically under each of the species—if attributable to a species—followed by yet another sequence of hybrid cultivars. It would be so much easier to find a particular name if there was a straight A-Z sequence of all the cultivars regardless of species.

There are many color photographs—especially close-ups of flowers—and this is a very valuable aspect of the book. A good photo or drawing says so much more than a wordy description, however detailed. It is so much simpler to identify plants distinguished on subtleties such as shape of floral markings when there is a good illustration. It is a pity that there is not an image of every cultivar! The authors must be congratulated for making a good job of a very difficult task.

*Brian Mathew
Claygate, Esher, Surrey, England*

BOOK REVIEW

Clivias. Harold Koopowitz. Forward by Sir Peter Smithers. Timber Press, Portland, OR. Hardcover, 384 pp., 118 color illus. (most by James Comstock), 3 charts, 1 b/w photo. \$34.95. ISBN 0-88192-546-2. 2002.

Clivias, those erstwhile Victorian favorites and California ubiquities, have enjoyed a renaissance of worldwide popularity in recent years, fueled in part by the relatively broad availability of once rare yellow-flowered cultivars. China and Japan's cliviophiles have a near obsessive fascination with dwarf, variegated, and other arguably monstrous forms, but, as Harold Koopowitz tells us in his new, comprehensive horticultural monograph, clivia obsession is not restricted to Asia.

The genus *Clivia* (Amaryllidaceae) consists of 5 (a new species has been described since this book went to press) semi-tender, shade-loving species of evergreen Amaryllidaceae that never form bulbs. Three of the species have tubular flowers, but it is around *C. miniata*, with open funnel-form perianths, which most aficionado's passion revolves. Clivias offer both attractive, dark-green strap-shaped foliage, and a spectacular floral display ranging through all shades of orange and yellow. The brightly colored berry fruits provide a secondary display after the flowers fade. Despite a reputation as connoisseur plants, they are remarkably tough and reasonably adaptable. Though only Californians can grow them outdoors in the U.S. with the ease of garden weeds, it is possible for anyone to enjoy their spectacular blooms indoors.

Harold Koopowitz, former executive director of the International Bulb Society, professor of ecology at The University of California, Irvine, and well-known breeder of orchids and *Narcissus*, has left no stone unturned in this handsome volume devoted to South Africa's forest lilies. Beginning with a history of the genus, and a discussion of its sometimes contentious nomenclature, Koopowitz describes each of the species in detail, along with an account of its more obscure sister genus, *Cryptostephanus*. A third chapter summarizes what is known about the biology of the genus. The rest of this book is devoted to the horticulture of clivias from virtually every angle imaginable, including a marvelous dissertation on color expression and inheritance. Clivia hybridization receives a full chapter discussion that should answer any question a prospective breeder might ask. In a chapter entitled "Clivia Obsession", we are treated to a personable cross-continental horticultural history of clivia fancy. Six full chapters are devoted to each class of clivia hybrids: standard orange and red miniatas, yellows, pastels, and those with variegated foliage, cyrtanthiflora-type hybrids (a class accu-

rately limited to *C. miniata* x *nobilis* crosses, but widely applied to *miniata* crossed with any of the other species), and finally, so-called “novelty” types (i.e., the “freaks”). The book is graced throughout with beautiful color photographs, mostly by the talented clivia hybridizer and photographer James Comstock. Koopowitz also projects the future of clivia development, carefully separating past breeder’s bombast concerning alleged “intergeneric” hybrids from the true possibilities that could be achieved. Finally, in a short appendix, we are treated to a biography of the woman commemorated in name by this regal amaryllid, Lady Charlotte Florentia Clive. A second appendix provides sources of further information as well as plants and seed.

Informative as this volume is, the writing throughout is also immensely readable. It is a rare horticultural monograph that can be enjoyed purely on its literary merits. Harold Koopowitz has not only provided the ultimate guide to knowing and growing clivias, he should be congratulated for raising the standard for this sort of book to a new level.

Alan W. Meerow
Miami, Florida

CONTRIBUTOR'S GUIDELINES FOR *HERBERTIA*

HERBERTIA is an international journal devoted to the botany and horticulture of geophytic plants. A special emphasis of the journal is the Amaryllidaceae and other petaloid monocot families rich in bulbous or cormous plants, but articles treating any aspects of dicotyledenous geophytes are welcome as well. Contributors are asked to follow the following guidelines when submitting papers. Manuscripts departing grossly from this format will be returned to the author(s) for revision.

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Eucrosia aurantiaca (Baker) Pax. Die Nat. Pflanzenfam.
(A. Engler and K. Prantl, eds.), 15a: 415 (1930).

Callipsyche aurantiaca Baker. Refug. Bot. 3:t. 167 (1869). Neotype:
Ecuador, El Oro, Ayabamba, 200 m, Andre 4262 (K).

Eucrosia morleyana Rose. Addisonia 7: 3-4, pl. 226 (1922). Type:
Ecuador, Chimborazo, Huigra, 4000 ft, Rose & Rose 22593 (holotype,
US; isotypes, GH, NY, S).

Eucrosia eucrosioides var. *rauhiana* (Traub) Traub. Pl. Life 22: 62 (1966).
Callipsyche eucrosioides var. *rauhiana* Traub. Pl. Life 13: 61 (1957). Type:
 Ecuador, Azuay, Pasaje, 300 m, Rauh & Hirsch E15 (holotype, MO)

Bulb large, 7.7-10 cm long, 6-7.7 cm in diam.; tunics tan-brown; neck (2.5)5-8 cm long, 2-2.6 cm thick. Leaves 2, hysteranthous; petiole 27-35 cm long, 7.5-10 mm thick, deeply channelled for most of its length; lamina ovate-elliptic, 29-40 (50) cm long, (12) 16-22 (29) cm wide, acute or short-acuminate, basally attenuate to the petiole, thick, coarsely undulate, hypostomatic, abaxial cuticle thickly striate and non-glaucous. Scape (5) 7-9(10) dm tall, ca. 10 mm in diam. proximally, ca. 4-6 mm in diam. distally; bracts 3(5) cm long, lanceolate. Flowers (7) 10-12 (13), zygomorphic, all reaching anthesis concurrently, more or less perpendicular to the axis of the scape; pedicels (11) 22-33 mm long, 1-2 mm in diam.; perianth (2.8) 3-4 (4.4) cm long, green in bud, yellow at anthesis, rarely orange or pink, compressed laterally giving the perianth a somewhat flattened appearance; tube sub-cylindrical, 5-7 mm long, ca. 5-6 mm wide, constricted at the ovary to ca. 3.8 mm wide, concolorous with the tepals for most of its length, green only at the base; tepals spreading dorsally and ventrally to 23-29 mm wide, recurved and sometimes stained green apically; outer tepals (20) 23-29 (36) mm long, 5-6 mm wide, apiculate, lanceolate, keeled, 2 of them situated laterally, one dorsally; inner tepals 20-26 (34) mm long, obtuse, oblanceolate-spatulate, margins undulate at the middle, 2 of them ca. 9.5 mm wide and situated laterally above the 2 lateral outer tepals, the third one 5-7 mm wide, ventrally declinate and with the lower lateral tepals forming a pseudo-labellum. Stamens subequal, 8.5-11 cm long, filiform, long-declinate, ascendent in their distal 1/4, green; filaments dilated and connate in their proximal 2-3 mm; globose nectar glands present at the perianth throat, each 1-2 mm in diam.; anthers 5.5-6 mm long, oblong; pollen green, the exine mostly tectate-perforate. Style 10-11 cm long, green; stigma less than 1 mm wide. Ovary ellipsoid, 6.5-9 mm long, 4-4.5 mm wide; ovules 20 or more per locule. Capsule 2.5-3 cm long, 17-22 mm in diam.; pedicel 5-6 cm long; seeds numerous, blackish-brown, ca. 6.5 mm long, 1.5 cm wide. $2n = 46$. Flowering July-September and December-January.

ECUADOR. El Oro: between Santa Rosa and La Chorita, 0-100 m, Hitchcock 21139 (GH, NY, US). Chimborazo: Río Chanchan canyon between Naranjapata and Olimpo, terrestrial in rock wall crevices, 800

m, (ex hort), Horich ISI # 214 (UC). Between Huigra and Naranjapata, 600-1200 m, Hitchcock 20638 (GH, NY, US). Cañar: valley of Río Cañar near Rosario, 960 m, Prieto CP-18 (NY, S). Azuay: Road from Jiron to Pasaje, near Uzhcurrumi, dry, steep, rocky hillside, 840 m, Plowman et al. 4600 (GH), Plowman 7634 (F), Plowman 12024 (F). Km 97 on road from Cuenca to Saraguro, dry thorn scrub, ca. 1100 m [incorrectly typed on specimen label as 2400 m], Madison et al. 7517 (SEL). - Inhabiting semi-desert and dry, rocky canyons and hills of the lower inter-Andean valleys (100) 300-900 (1100) m. Endemic.

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Alan W. Meerow, Editor
HERBERTIA
USDA-ARS-SHRS
13601 Old Cutler Rd.
Miami, FL 33158
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